# The ins and outs of manioc diversity in Gabon, Central Africa: A pluridisciplinary approach to the dynamics of genetic diversity of Manihot esculenta Crantz (Euphorbiaceae)

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# The ins and outs of manioc diversity in Gabon, Central Africa

A pluridisciplinary approach to the dynamics of genetic diversity of *Manihot esculenta* Crantz (Euphorbiaceae)

Thesis submitted for the degree of
**Doctor of Philosophy**

by

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based on research carried out under the supervision of
Dr. Trevor Hodkinson

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# Declaration

I thereby certify that this thesis is a record of my original work and has not been previously submitted as an exercise for a degree at this or any other university. All sources of information have been appropriately acknowledged.

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Marc Delêtre

Last revised March 2011.

## Summary

Manioc (*Manihot esculenta* Crantz subsp. *esculenta*, Euphorbiaceae) is the staple food and livelihood of more than half a billion people around the world, and ranks third, just behind rice and maize, as a source of calories in the tropics. Manioc was originally domesticated in the southern rim of Amazonia, and was introduced into Africa from Brazil by the Portuguese in the 16$^{th}$ century. Four hundred years later, it is now a major staple crop throughout Africa, and reached similar levels of genetic diversity to those encountered in its area of domestication, suggesting that despite the bottle-neck following its introduction, any losses of genetic diversity have been balanced by processes of restoration. Despite the economic importance of the crop in Africa, few studies have attempted to elucidate the origin of this diversity. This thesis addresses the mechanisms behind the secondary diversification of manioc in Africa.

Manioc is propagated clonally, by way of stem cuttings, but has maintained its sexual fertility. Sex enters the plant's cycle when farmers choose to incorporate self-sown 'volunteer' plants originating from true seeds into their stocks of clones. The major role played by sexual reproduction in the domestication and diversification of several vegetatively propagated crops has become increasingly recognized. Much less is known, however, of similar interactions between farming practices and the biological traits of the crops in their areas of introduction. Because manioc sexual reproduction is not of immediate use to farmers, knowledge of the plant's intimate biological traits is intricately linked to the relationship of farmers to the plant, and diversity, in turn, is dependent on this knowledge. In Africa, the relative contribution of each component (sexual and asexual) of the plant's reproductive biology thus depended greatly on farmers' intimate perception and valuation of diversity, which depended, in turn, on the processes through which African farmers have built their own folk ecological knowledge of the crop.

The patterns of folk reasoning with respect to the management of manioc volunteers in African farming settings were examined through a series of village-level studies of traditional manioc farming systems in Gabon, central Africa. Combining ethnobotanical and population genetic studies of local nomenclature systems of manioc landraces, the role of small-scale farmers as the possible 'architects' of the crop's secondary diversification in Africa was explored through the comparative study of ten communities of manioc farmers in Gabon.

Africa’s complex history and multiplicity of cultures has played a major part in shaping the high diversity of manioc in Gabon, and results show that cultural diversity accounts in part for the strong regional disparities in varietal richness of manioc. Results suggest also that present patterns of manioc diversity in Gabon have been conditioned, to a large extent, by the joined history of the plant and the people. In this reciprocal interaction, the modes of diffusion of manioc in Africa have had a determining influence that still shows in variations among populations in their perception and valuation of manioc diversity. History, therefore, was an important factor in the emergence of Africa as a secondary centre of diversity for manioc. General findings are summarized and discussed in the broader context of farmer-plant interactions and their importance for the evolutionary dynamics of genetic diversity in vegetatively propagated crop plants.

***“They say a little knowledge is a dangerous thing,***
***but it's not one half so bad as a lot of ignorance”.***
*T. Pratchett.*

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This is not a thesis about a plant. This is all about people.
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From 53°19′59″N 6°14′56″W to 0°23′24″N 9°27′15″E and back, as far as 37°46′45″N 122°25′9″W and 59°21′N 18°04′E, the last four years have been an endless wander. I went downstream into the maze of the mangroves of the Ogooué to meet the man “who did not want to see Libreville”, I drank the mangrokom in the Woleu-Ntem on the sounds of the balafons, watching over skies full of glow-worms and stars the names of which I didn’t know. I wandered in the bare lands of the Bateke plateaux, and stepped on the barren Giant’s Causeway.

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# Foreword

My study concerns the evolutionary dynamics of manioc (*Manihot esculenta* subsp. *esculenta*), a crop plant introduced into Africa only four centuries ago. For a study in the field of ecology and evolutionary biology, the format and the content of this thesis may at first surprise the unwary reader. Some parts may seem more suitable for a dissertation in the field of history or anthropology than for a dissertation which primary foci are ecology and evolution. However, many recent studies have shown that the "environment" in which cultivated plants evolve is complex, and that much can be learned from approaching the question in terms of people-plant interactions (Anderson 1960, Salick 1995), and doing so by stretching the breadth of the topic beyond that usually presented in a thesis on ecology.

History, in particular, is an important dimension to consider in explaining patterns of genetic diversity in cultivated plants, especially in the case of manioc whose introduction and diffusion into Africa foreshadowed and accompanied the drastic socioeconomic transformations of African societies following the onset of formal colonial rule in the late 19th-early 20th centuries. This idea that external factors, including the vectors and modes of manioc spread, have had a considerable influence on the processes of re-appropriation of the new crop by local populations (that I termed later "cultural domestication") is central to this study.

This dissertation is an interdisciplinary approach to the evolutionary dynamics of genetic diversity in crop plants. This first chapter introduces the general context of my research, and introduces some of the concepts behind the formulation of the questions that the thesis builds upon. I also present some background information on manioc, the model chosen to explore the question of people-plant interactions. Finally, I outline the aims and the structure of my thesis.

**Plate I**

***Manihot esculenta*** **Crantz**. Illustration by L. Müller, from Brandt W, Gürke M, Köhler FE, Pabst G (ed.), Schellenberg G, Vogtherr M (1887) *Köhler's Medizinal-Pflanzen in naturgetreuen Abbildungen mit kurz erläuterndem Texte. Atlas zur Pharmacopoea germanica, austriaca, belgica, danica, helvetica, hungarica, rossica, suecica, neerlandica, british pharmacopoeia, zum Codex medicamentarius, sowie zur Pharmacopoeia of the United States of America*. Gera-Untermhaus. 506pp.

# Chapter I

## *"The strange and the bizarre"*

***"To adopt a new food plant (…)***
***is not to adopt the complex culture surrounding it".***
*W.O. Jones (1957).*

## Notes

**1.** Although the two words exist in English, and although both are generally accepted, I followed Gade (2002) in his choice to favour the appellation ‘manioc’ rather than ‘cassava’, and used manioc throughout this thesis when talking of the crop, *Manihot esculenta* Crantz sbsp. *esculenta*.

**2.** Terms denoted with an asterisk * are defined in the glossary shown in Appendix D.

# 1. Towards the concept of agrobiodiversity

Genetic diversity is the raw material of variation, and the warrant of crop future (Frankel & Soulé 1981). Understanding the distribution of crop genetic diversity and its dynamics are essential for developing *ex situ* (off-site) and *in situ* (on-site) strategies for preserving crops' adaptative potential (Brush *et al.* 1995). In the wake of de Candolle (1883), Nikolaĭ Ivanovich Vavilov was among the first to cast light on the geographical distribution of crop genetic diversity.

## 1.1. From Vavilov to Harlan: centres and noncentres

Between 1916 and 1933, Vavilov led several plant-collecting expeditions throughout the world to gather seeds of potential use for the development of plant breeding and agriculture within the former USSR, and observed that the genetic diversity of crop relatives is concentrated in particular geographical areas, that he termed 'gene centres'. By studying the geographical range of distribution of the crops and determining those areas where the greatest number and diversity of races, varieties and the nearest wild relatives of the crops are to be found, Vavilov identified eight world centres of crop diversity, and postulated that these regions correspond to regions where the crops were originally domesticated (Vavilov 1926).

Vavilov's theories were later questioned and the definition and delimitations of his original centres of origin considerably re-evaluated (Zukhovsky 1968, Harlan 1971, Zeven & de Wet 1982, Hawkes 1983), but his work was pioneering and has remained influential. After him, Harlan (1951) suggested that the concept of 'centre' proposed by Vavilov was too restrictive, and showed that, within Vavilov's centres, high geographical variability in varietal diversity* can be found. Harlan thus pinpointed "microgene centres", where enormous variation is concentrated, abutting areas of contrasted low varietal diversity. Later, he proposed that 'noncentres' of agricultural origins be also recognized (Harlan 1971). His idea that agriculture may have originated over vast areas, rather than 'centres', opposed the implicit narrow geographical definition of Vavilov's centres. Harlan thus defined three independent systems, each of which associates a centre of diversification and a large and diffuse 'noncentre' of diversity.

## 1.2. Primary and secondary centres of diversity

In his original theory of the centres of origin of cultivated plants, Vavilov (1926) emphasized the connection between centres of diversity and centres of origin, but he realized that the centre of domestication of a crop and its centre—or centres—of diversity have only a loose connection, and that considerable genetic and phenotypic diversity can be also found outside the primary centre of origin. Vavilov afterwards distinguished primary centres of diversity, where the crops were actually domesticated, and secondary centres, where diversification arose following the diffusion of the crops outside their centre of domestication.

### 1.2.1. The role of the Columbian exchange

Several examples of secondary diversification have been documented, *e.g.*, *Citrus* spp. in Europe (Ollitrault & Luro 2001), watermelon (*Citrullus lanatus* [Thunb.] Mats. & Nakai, Cucurbitaceae) in Brazil (Romão 2000), peanut (*Arachis hypogaea* L., Fabaceae), bean (*Phaseolus vulgaris* L., Fabaceae), barley (*Hordeum vulgare* L., Poaceae), banana (*Musa* spp.), and manioc (*Manihot esculenta* Crantz subsp. *esculenta*, Euphorbiaceae) in Africa (Smartt & Simmonds 1995, Pickersgill 1998).

Many secondary diversifications hail from the widespread exchange of plants, animals, diseases and ideas that took place between 1500 and 1900 between the Americas, Africa and Europe, following the discovery of the Americas by Christopher Columbus in 1492. Intensive exchanges during the transatlantic slave trade facilitated the introduction into Africa of several American crops, including maize (*Zea mays* L. ssp. *mays*, Poaceae), peanut, cacao (*Theobroma cacao* L., Malvaceae), bean, sweet potato (*Ipomoea batatas* [L.] Lam., Convolvulaceae), and manioc, while conversely several crops from Europe and Africa were also introduced into the New World, including wheat (*Triticum aestivum* L. subsp. *aestivum*, Poaceae), chickpea (*Cicer arietinum* L., Fabaceae), melon (*Cucumis melo* L. subsp. *melo*, Cucurbitaceae), onion (*Allium cepa* L., Alliaceae), radish (*Raphanus sativus* L., Brassicaceae), and grapevine (*Vitis vinifera* L., Vitaceae).

### 1.2.2. Human diversity begets crop diversity

By favouring cross-cultural exchanges (*sensu* Harris 1998) of cultivated plants between Africa, the Americas and Europe, this “Columbian exchange” (Crosby 1973) has favoured the emergence of several secondary centres of crop diversity.

Secondary diversification where societies who have adopted the new crops have developed a curiosity for the new plants and purposely maintained these different types in their fields (see the example of groundnuts in Africa, in Bunting 1990).

## 1.3. The role of small-scale farmers

Vavilov (1926) was already aware of this connection, but it is only after W.G. Rosen coined the term 'biodiversity' in 1985, during the first meeting of the National Forum on Biodiversity, in Washington, that the role of small-scale farmers as the first 'engineers' of crop diversity, in the plants' area of domestication as in their areas of introduction, has been brought to international awareness.

Small-scale farmers maintain in their farms* a large diversity of cultivated species, and recognize many different types within each of their crops (Boster 1984a, 1984b, Brush *et al.* 1995, Shigeta 1996, Salick *et al.* 1997, Emperaire *et al.* 1998, Elias *et al.* 2000a, McKey *et al.* 2001, Peroni & Hanazaki 2002, Zaldivar *et al.* 2002, Manusset 2006, Sardos *et al.* 2008). In the world, there are an estimated 200,000 or more such varieties of rice (*Oryza sativa* L., Poaceae), and about as many varieties of wheat (FAO 1998). The FAO estimates there are about 47,000 varieties of sorghum, 30,000 varieties each of common bean, chickpea, and maize, 20,000 varieties of pearl millet, 15,000 varieties of peanut, and between 7,000 and 9,000 varieties of manioc.

## 1.4. The multifunctional role of diversity

This agricultural biodiversity, also called "agrobiodiversity" (FAO 1999), is the warrant of flexibility in local farming systems (Harlan 1975). For modern breeders, it is the genetic reservoir from which new traits can be selected to develop new cultivars* with desired characteristics (*e.g.*, disease resistance). For farmers, maintaining different types of the same crop is a common strategy to remain flexible when faced with heterogeneous and unpredictable environments. Diversity maintains the crop's adaptive potential and buffers the effects of unpredictable changes in the environment (Peroni & Hanazaki 2002). It ensures that, within the large diversity of varieties that farmers maintain, at least a few will resist sudden outbreaks of epiphytotics[1].

[1] Examples of epiphytotics include the potato blight (*Phytophthora infestans* [Mont.] de Bary) in early 19th century Ireland, and the current pandemics of Cassava Mosaic Virus (CMV) disease in Africa. Along with the Cassava Bacterial Blight (CBB) (*Xanthomonas campestris* pv. *manihotis* [Berthet & Bondar] Dye), the CMV, a plant pathogenic virus of the Geminiviridae family, is one of the major threats to manioc agriculture in Africa (Legg & Fauquet 2004).

Diversity also performs ecological services (*e.g.*, prevention of soil erosion, renewal of soil fertility) necessary to ensure the system's resilience (Altieri 1999). Diversity is finally favoured from a simple cultural stand point (Caillon & Degeorges 2007). Small-scale farmers are, in this sense, 'collectors', and their valuation of diversity in their farms is also motivated on grounds that go beyond simple risk aversion (Emperaire & Peroni 2007). The non-purposive grounds of valuation of diversity in small-holders' farms have been highlighted in several studies, on taro (*Colocasia esculenta* [L.] Schott, Araceae) in Vanuatu (Caillon & Degeorges 2007), on ensete (*Musa ensete* (Welw.) Cheesman, Musaceae) in Ethiopia (Shigeta 1990, 1996), on groundnuts in Africa (Bunting 1990 and references therein), and on manioc in Amazonia (*e.g.*, Boster 1984b, Elias *et al.* 2000a, Emperaire & Peroni 2007, Heckler & Zent 2008), in Peru (Salick *et al.* 1997), and in Vanuatu (Sardos *et al.* 2008).

In their farms, farmers dynamically manage this diversity by continually collecting, testing, selecting, and exchanging new strains with unusual and interesting traits. Examples include potato (*Solanum* x *ajanhuiri* Juz. & Bukasov) in Bolivia (Johns & Keen 1986), sorghum (*Sorghum bicolor* [L.] Moench, Poaceae) in Cameroon (Alvarez *et al.* 2005, Barnaud *et al.* 2007), maize in Mexico (Louette 1994, Perales *et al.* 2003), yams (*Dioscorea* spp., Dioscoreaceae) in Benin (Scarcelli *et al.* 2006), manioc in Peru (Salick *et al.* 1997), Guyana (Elias 2000) and Brazil (Sambatti *et al.* 2001), and wheat in Turkey (Brush & Meng 1998). At the community level, farmers apply a set of rules to characterize and classify this diversity into culturally meaningful and tangible units—the landraces.

## 1.5. The paradigm of landrace

### 1.5.1. Harlan's definition

Several definitions of landraces, variously termed in the literature as "folk varieties" or "ethnovarieties", have been proposed (see a review in Zeven 1998). Harlan (1975) proposed the following definition:

*"Landraces have a certain genetic integrity. They are recognizable morphologically; farmers have names for them and different landraces are understood to differ in adaptation to soil type, time of seeding, date of maturity, height, nutritive value, use and other properties. Most important, they are genetically diverse"*.

### 1.5.2. Mayr's definition

Earlier, Mayr (1937) suggested a classification of landraces into five categories, based on the geographical origin of landraces:

1. *Autochthonous landraces*, defined as long-established landraces within the farming system considered, indigenous to the region considered;
2. *Autochthogenous landraces*, which derive from a new genotype (spontaneous mutant or sexual recombinant);
3. *Allochthonous landraces*, which were bred outside the considered region and introduced through exchanges;
4. *Allochthogenous landraces*, which were grown for a long period in a non-native region, and which adapted to their new environment;
5. *Cultivars*, that is, a variety that has been created and/or selected through formal breeding.

The advantage of Mayr's distinction between autochthonous and autochthogenous is that it clearly emphasizes the local origin of the latter, by taking into account the breeding history of landraces. This is particularly important in the case of vegetatively propagated crops, especially in their areas of introduction, where all landraces are, in theory, allochthonous. However if—as in the case of manioc—the plant has retained its ability to reproduce sexually, the selection, conscious or unconscious, of plants derived from spontaneous recombination may also generate autochthogenous forms of diversity.

Given the complexity and specificity of the life cycle of each crop, it is difficult to give a general definition of a landrace. Zeven (1998) proposed that the reproductive biology of the crop, as well as the methods for harvesting and selecting planting material, be reintegrated in the definition of the landrace, as these factors influence its genetic composition most.

Because what I am interested in is the role of farmers in maintaining and creating diversity outside a crop's original range of distribution, I will adopt Harlan's general definition of landraces, while keeping Mayr's distinction between landraces according to their breeding history.

# 2. The particular case of crops with a mixed reproductive system

In the process of evolution under human selection, domesticated plants underwent several transformations, losing wild characters and evolving new traits, exhibiting a large diversity of forms, and becoming often strikingly different from their wild progenitors. In several clonally propagated crops, a regular consequence of this "domestication syndrome" (Harlan 1975) has been the loss of their ability to reproduce sexually (*e.g.*, some taros, bananas, and some yams). Manioc, along with some other crops (*e.g.*, potato, sweet potato, and some yams) has however maintained, at least partly, its sexual fertility (Cours 1951, Jennings 1963, Silvestre & Arraudeau 1983).

## 2.1. The domestication of manioc

### 2.1.1. Origin of domestication

Manioc (*Manihot esculenta* Crantz subsp. *esculenta*, Euphorbiaceae) is a perennial shrub, cultivated pantropically for its starchy roots. The crop was probably domesticated over 8,000 years ago (Piperno & Holst 1998) from a single wild ancestor, *Manihot esculenta* subsp. *flabellifolia* (Pohl) Ciferri (Allem 1994, 1999, Allem *et al.* 2001, Roa *et al.* 1997, Olsen & Schaal 1999, 2001, Roa *et al.* 2000, Olsen 2004). Initially, Vavilov (1926) located the centre of domestication of manioc in north-eastern Brazil. Recent studies however suggest that the centre of domestication of manioc is most likely restricted to the southern rim of Amazonia (Olsen & Schaal 2001, Olsen 2004, Léotard *et al.* 2009).

Domestication has induced several changes in manioc. First, the morphology of the roots—the part of the plant which is of greatest interest to farmers—has evolved. The roots have became larger, with a higher dry matter content and higher starch content, but conversely lower protein content, typically 1-2% compared to 10-15% in the wild relative (Jennings 1995). Manioc roots also contain variable amounts of cyanogenic glucosides, but curiously, cyanogenesis was not always counter-selected by farmers.

### 2.1.2. The bitter-sweet polarity

Between 3,000 and 12,000 known plant species are cyanogenic, among them a number of economically important plants such as sorghum, almonds (*Prunus dulcis* [Mill.] D.A. Webb, Rosaceae), Lima beans (*Phaseolus lunatus* L., Fabaceae), white clover (*Trifolium*

*repens* L., Fabaceae), rubber tree (*Hevea brasiliensis* Müll. Arg., Euphorbiaceae), some yams (*Dioscorea* spp.), and manioc. Manioc, however, is probably the sole widely cultivated crop that is actually highly toxic (McKey & Beckerman 1993).

All manioc cultivars are, to various extents, cyanogenic (de Bruijn 1973, McMahon *et al.* 1995), but in many parts of South America (Dufour 1988, Narváez-Trujillo *et al.* 2001, Elias 2000, Henry & Hershey 2002) and Africa (Chiwona-Karltun *et al.* 1998), farmers recognize two types. Roots are usually called "sweet" if they contain below 100mg of cyanogenic glucosides (CG) per kilogram fresh weight (FW). Above 100mg, roots are considered "bitter" (Dufour 1988). The CG contents of manioc roots, however, can reach up to 500mg.kg$^{-1}$ FW in the most toxic cultivars.

Manioc produces two kinds of cyanogenic glucosides: linamarin, the more abundant (more than 90% of the glucosides), and lotaustralin, which accounts for less than 10% (McMahon *et al.* 1995). To remove cyanides, farmers have developed various techniques (for a review, see Lancaster *et al.* 1982), which involve grating, pressing and/or cooking manioc roots. In manioc, linamarin is stored in cell vacuoles. The cells contain also two enzymes, linamarase, a $\beta$-glucosidase, and a hydroxynitrile lyase (HNL), both located in the cell wall (McMahon *et al.* 1995). The breaking down of cells during grating puts the enzymes in contact with their substrates. When linamarin is hydrolyzed by linamarase and hydroxynitrile lyase, free cyanide (HCN) is released. Most of the HCN, which is highly soluble and volatile, is eliminated during juice extraction (pressing) and later during cooking, bringing HCN contents to safe levels[2].

In South America, bitter and sweet manioc have distinct geographical distributions (Renvoize 1972), and bitter and sweet manioc were long believed to be two different species (Rogers 1965). Whether both kinds evolved independently, simultaneously, or sequentially (bitter before sweet or sweet before bitter), is however still highly debated (de Bruijn 1973, McKey & Beckerman 1993). Because the range of concentrations in cyanogenic glucosides in cultivated manioc far exceeds that encountered in any wild *Manihot* species, McKey and Beckerman (1993) suggested that high and low cyanogenic manioc types probably evolved under the diversifying selection of manioc farmers, and that the bitter-sweet polarity in manioc is a "by-product" of domestication, reflecting variations in cultural preferences for bitter or sweet manioc[3].

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[2] The lethal dose is comprised between 50-60mg, ca. 1mg per kg bodyweight (Bolhuis 1954).

[3] This will be further discussed in Chapter IV.

## 2.2. Domestication and the (near) loss of sexuality

Because manioc is propagated mainly clonally, by way of stem cuttings, the domestication of manioc was also followed by modifications in the plant's architecture. Unlike its wild relative, manioc is characterized by large stems which branch less, and are more adapted to clonal reproduction (Jennings 1995, Elias *et al.* 2007). The manioc plant grows as a succession of orthotropic (upright-growing) modules, separated by di- or trichotomic ramifications, following the architectural model of Leeuwenberg (Hallé *et al.* 1978). Branching is induced by flowering. The apical meristem terminates to produce inflorescences, while growth is resumed through lateral meristems.

### 2.2.1. Clonal versus sexual fecundity

Sexual fecundity, therefore, is positively correlated with the degree of ramification of the plant (Jennings 1995). Every time the plant branches the diameter of the stem diminishes. "Clonal fecundity" (Elias *et al.* 2007), that is, the aptitude of the plant to produce stems suitable for the preparation of stem cuttings, thus directly depends on the plant's architecture and conflicts with sexual fecundity. Farmers compensate for the reduction in diameter by chopping longer pieces of stem. However, Elias (2000) demonstrated that below one cm of diameter, the cutting is too small and withers rapidly in the field. Because of these physical constraints which delineate the optima for the quality of cuttings, there is only a certain length of the stem that farmers can use to prepare stakes. For manioc farmers, there was therefore some interest in the plant losing its ability to reproduce sexually.

### 2.2.2. The benefits of sex

In fact, both sexual and clonal reproduction present advantages to farmers. On the one hand, farmers want to maintain their landraces' characteristics in the most homogeneous and stable configuration. Clonal propagation, in this case, is the best option. On the other hand, it is important that the crop maintain its adaptive potential, which requires maintaining high levels of genetic diversity. A strictly clonal propagation system is able to maintain a high diversity of alleles per locus, by protecting polymorphism within a fixed state of heterozygosity (Balloux *et al.* 2003). However, every time the crop is propagated, be it under human or natural selection, or by genetic drift*, some genotypes are lost, and with time genotypic and allelic diversity decrease (Balloux *et al.* 2003).

In addition, manioc cuttings accumulate deleterious mutations with time, a process known in evolutionary genetics as "Müller's ratchet" (Felsenstein 1974). Recombination, through sexual reproduction, permits stirring the genetic pool to produce new combinations of alleles, thereby increasing diversity, but also reducing the deleterious effects of the 'genetic load' of mutations in clonal lineages. For small-scale farmers, the mixed reproductive system of manioc means they can maintain those genotypes which they most like, while still being able to select new ones issued from sexual reproduction.

Sex enters the plant's cycle when farmers choose to incorporate self-sown 'volunteer'[4] plants, originating from true seeds, into their stocks of clones. Because each plant resulting from sexual reproduction is genetically unique, the incorporation of volunteer plants increases genetic diversity of the crop population, creating new combinations of traits and compensating for the slow loss of genotypes that would be associated with purely clonal propagation (Balloux *et al.* 2003), when only a subset of genotypes is used as the clonal parents of the next generation.

## 2.3. Manioc reproductive biology

Manioc is monoecious and preferentially allogamous (Da Silva *et al.* 2003). Inflorescences are protogynous (female flowers open one or a few weeks before male flowers), favouring cross-pollination. Each inflorescence produces between one and six fruits, each of which contains three carunculate seeds (Raffaillac & Second 2001). Seeds are dispersed by autochory (explosive dehiscence; Rogers 1965), followed by myrmecochory (dispersal of seeds by ants[5]; Elias & McKey 2000). Manioc seeds can lie dormant for several decades (up to 50 years; Elias 2000). In traditional shifting cultivation[6] farming systems, dormancy of manioc seeds is broken by an elevation of soil temperature which follows removal of vegetation.

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[4] By "volunteer", I refer to self-sown manioc plants that emerge in farms from a seed bank formed in the previous cultivation cycles.

[5] Myrmecochory has not been reported yet for African manioc.

[6] Slash-and-burn shifting cultivation, also called swidden cultivation (see Bahuchet & De Maret 1994) involves the clearing of a parcel of forest, then burning the dried vegetation to prepare the land for cultivation. Burning helps remove weeds and can add nutrients to the soil. In shifting-cultivation farming systems, the land is left afterwards to fallow for an indefinite length of time, decided by farmers and influenced by external constraints (land availability), until the soil is deemed to have recovered its fertility. The plot can then be cleared again for another cultivation cycle to take place.

When they clear and burn new farms in secondary forest, farmers stimulate the germination of manioc seeds accumulated during the previous cultivation cycles (McKey *et al.* 2001, Pujol *et al.* 2002), and seedlings appear within two weeks of burning (Pujol *et al.* 2002). Studies of the germination ecology of manioc (Pujol *et al.* 2002) and comparative studies of manioc volunteer seedlings (Pujol *et al.* 2005a) suggest that adaptation of germination ecology to disturbed environments, already present in manioc's wild ancestors, could have favoured the maintenance of these traits in swidden agriculture farming systems, while the morphology of volunteers appears to have evolved towards forms more adapted to agricultural environments, under the unconscious selection exerted by manioc farmers.

### 2.3.1. The role of sexuality in magnifying genetic diversity

Manioc seedlings are the main available source of *de novo* diversity at the local scale (Cury 1993, Sambatti *et al.* 2001). In populations of manioc grown by Amerindians in Amazonia, high levels of genetic diversity are maintained by the regular incorporation of volunteer seedlings as new landraces, or as new clones within a named landrace (Elias *et al.* 2001a, 2001b). By 'freezing' interesting strains in a fixed state which can be reproduced indefinitely, clonal propagation of manioc volunteers has also the potential to create a huge diversity. The major role played by sexual reproduction in the diversification of manioc in Amazonia has become increasingly evident (Boster 1984b, McKey & Beckerman 1993, Salick *et al.* 1997, Elias *et al.* 2000a,b, McKey *et al.* 2001, Sambatti *et al.* 2001, Pujol *et al.* 2005b, 2007, Duputié *et al.* 2009b), and similar examples exist in other crops such as sweet potato (Yen 1974), potato (Johns & Keen 1986, Brush *et al.* 1995) and ensete (Shigeta 1996).

### 2.3.2. The role of folk ecological knowledge

The domestication syndrome resulted from farmers' keen eye for variation and active selection of the "strange and the bizarre" (Harlan & De Wet 1971). In the process of diversification of vegetatively propagated crops, the relative contribution of each component (sexual and asexual) of the plants' reproductive biology has however depended greatly on farmers' intimate perception and valuation of diversity. Because sexual reproduction is not of immediate use to farmers, knowledge of the plant's intimate biological traits is intricately linked to the relationship of farmers to the plant, and diversity, in turn, is dependent on this knowledge.

Anderson (1960) defined domestication as a "person-plant interaction". In the case of vegetatively propagated crops, his view of the domestication process is even more relevant. Unlike in the case of cereal cultivation, where plants are treated as 'bulk', clonal propagation creates a more intimate connection between the farmer and the plant, a direct person-plant "relationship" (Salick 1995), as each plant is treated and selected individually. The nature of this relationship created favourable grounds for farmers to observe, experiment with and learn about manioc.

Farmers' deep understanding of the manioc's biological traits and their potential for interacting with the plant, through a continuous process of selection of which the domestication syndrome is the epitome, is what I will hereafter refer to as folk ecological knowledge, also variably found in the literature as "indigenous knowledge", "indigenous technical knowledge", "local" or "traditional knowledge". Warren (1991) gave the following definition:

"*Indigenous knowledge (IK) is the (…) knowledge that is unique to a given culture or society (…). It is the basis for local-level decision making in agriculture (…), food preparation, (…) and natural-resource management*".

All other definitions that have been proposed emphasise the location and culture specificity of folk ecological knowledge and its dynamicity. Folk ecological knowledge evolves through experimentation—by doing, watching, and learning—and adapts to different cultural and social environments (Ellen & Harris 1996).

Much has been written about folk knowledge, and it is beyond the scope of this thesis to explore the concept further. I will simply point to the fact that, while the role of farmers' indigenous knowledge in maintaining and magnifying the diversity of local crops has been increasingly recognized (Warren 1992), much less is known of similar interactions between farming practices and crops' biological traits in their areas of introduction.

# 3. The puzzling question of manioc diversity in Africa

Manioc in Africa is a pertinent model for the investigation of these questions. The introduction of a crop outside its native range is often accompanied by a loss of genetic diversity, as only a sub-sample of the total genetic diversity present in the area of origin is transferred to the new areas. However, in the case of vegetatively propagated crops, a cultural factor can also accentuate the loss of genetic diversity, the non-diffusion of folk ecological knowledge present in the area of origin, and central to the maintenance of the crop's diversity.

## 3.1. Manioc in Africa

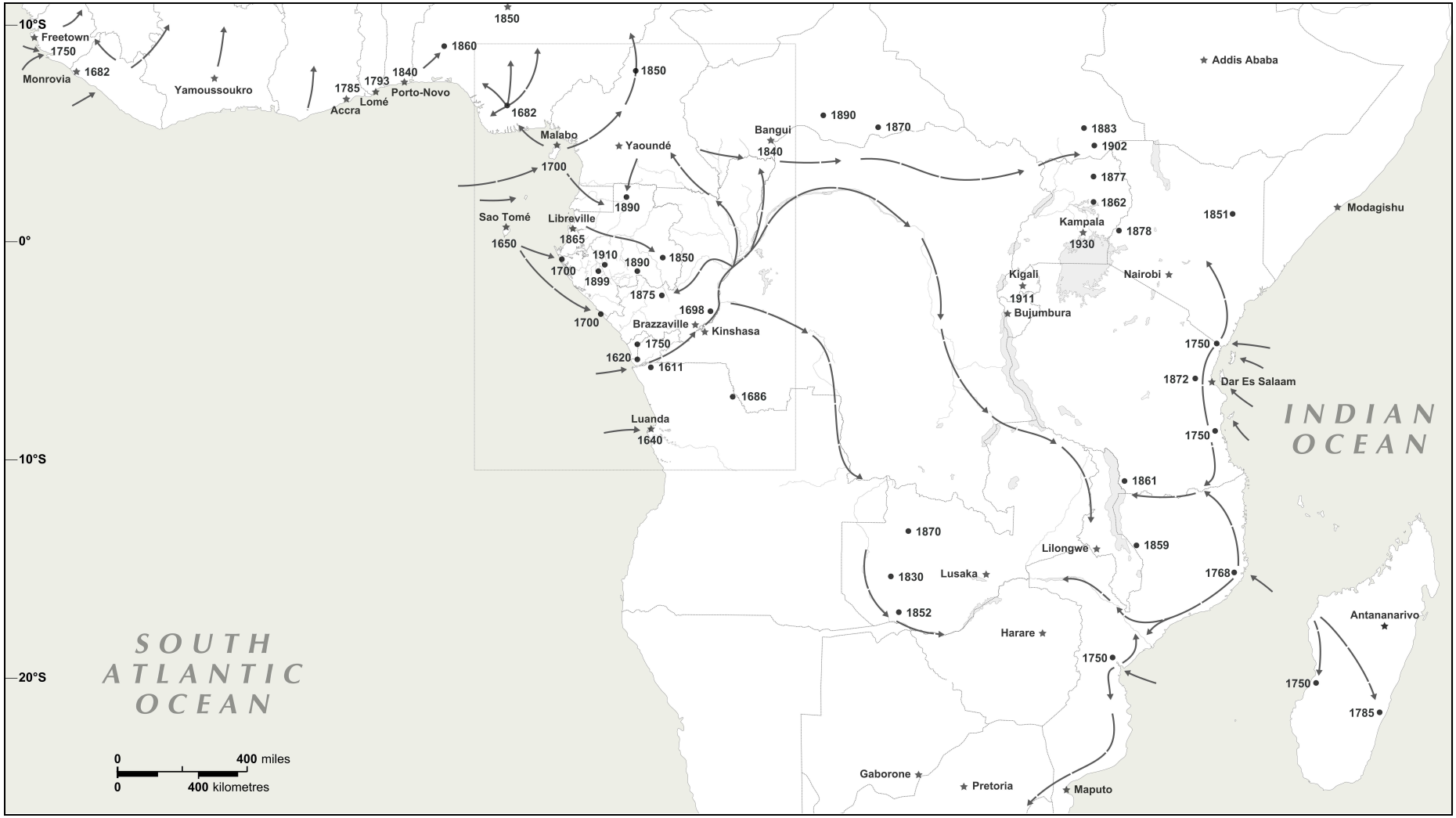
Manioc is the staple food and livelihood of more than half a billion people around the world, and ranks third, just behind rice and maize, as a source of calories in the tropics (FAO 2009). In Africa, manioc is grown in 39 countries, forming a 'manioc belt' that extends from Madagascar, in the south-east, to Senegal, in the north-west. With 104 MT in 2007, manioc production in Africa has surpassed that of Asia and South America (FAO 2009). Nigeria, Ghana, DR Congo, Ivory Coast, Uganda and Tanzania account together for 70% of manioc total production in Africa (Nweke *et al.* 1994).

### 3.1.1. The introduction of manioc in Africa

Manioc was first introduced to Africa in the second half of the 16$^{th}$ century (Jones 1959), but its diffusion moved in fits and starts, and took in total almost 400 years to complete (Map 1.1). In Central Africa, the diffusion of manioc was initially carried out mainly—or solely—by Africans themselves (Jones 1959). Through a phenomenon of cultural impregnation, facilitated by the strong ties between the Portuguese settlers and the kingdom of Kongo, manioc spread rapidly along the Congo River (Jones 1959), and was firmly adopted in most central African countries by the end of the 18$^{th}$ century.

Manioc was reintroduced along Africa's east coast in the 1750s, in Madagascar and in Mozambique (Jones 1959), but like in West Africa, it did not spread much up until the 19$^{th}$ and 20$^{th}$ centuries. Cultural and environmental barriers seem to have considerably impeded its diffusion[7] (Carter *et al.* 1992).

[7] Examples of cultural barriers to manioc adoption are discussed in Chapter IV.




**Map 1.1. Manioc hypothesized pathways of diffusion in Africa.** The historical trajectory of manioc in Africa was reconstructed from a literature review. Places and dates from the earliest mentions of manioc cultivation are reported on the map (modified from Carter *et al.* 1992). See Map 6.1 for details on the diffusion of manioc in Gabon and central Africa (excerpt).

Manioc diffusion continued in post-colonial times, and manioc reached its geographical limits (30°N-30°S) in the second half of the 20th century (Carter *et al.* 1992). In Congo RDC in the early 1960s (Fresco 1986), and in Mozambique in the 1980s (Carter *et al.* 1992), political instability and civil wars persuaded farmers to abandon their traditional cereals (millet, sorghum) and focus on manioc, a crop that was more dependable and less subject to seasonal variations (Fresco 1986, Carter *et al.* 1992, Bahuchet & Philippson 1998, Cloarec-Heiss & Nougayrol 1998, Cordell 2002).

### 3.1.2. The diversity of African manioc

Since it was introduced from Brazil in the 16th century (Jones 1959), manioc in Africa has reached levels of genetic diversity[8] similar to those encountered in Amazonia (Beeching *et al.* 1993, Fregene *et al.* 2000, 2003), suggesting that despite the bottle-necks* following introduction and the CMV pandemic (Kizito *et al.* 2005), any losses of genetic diversity have been balanced by processes of restoration. Manioc in Africa could have, in fact, undergone a secondary diversification process (Lefèvre & Charrier 1993, Pickersgill 1998), but despite the economic importance of manioc in Africa, few studies have attempted to elucidate the origin of this diversity (but see Lefèvre & Charrier 1993, Kizito *et al.* 2007, Manu-Aduening *et al.* 2005, Fregene *et al.* 2003).

## 3.2. The mechanisms of secondary diversification

Pickersgill (1998) proposed several mechanisms to explain secondary diversification, based on how diversity in secondary centres compares with the diversity found in the crop's area of origin:

1. Secondary centres characterized by a large diversity of novel forms, endemic to the area of introduction (*i.e.*, not found in the area of origin);
2. Secondary centres characterized by a large diversity of new combinations of characters, only found discretely distributed within the area of origin;
3. Secondary centres characterized by a concentration of diversity within the area of introduction, but no novel characters.

Different scenarios can explain the emergence of these different patterns of diversity in the crops' areas of introduction (Table 1.1).

[8] As measured with neutral molecular markers.

**Table 1.1. Mechanisms responsible for the emergence of secondary centres of diversity** and their consequences for diversity (modified from Pickersgill 1998).

| Mechanism | Factors | Consequences |
|---|---|---|
| **1. Rapid expansion** | Initial bottleneck<br>Founder effects*<br>Relaxed selective pressures | Novel characters |
| **2. Repeated introductions** | Limited bottleneck | Spatial concentration of diversity |
| **3. Hybridization** | | |
| a. Between genetically diversified types of the same crop | Recombination | Reshuffling of characters |
| b. Between introduced crop and local wild species | Introgression | Novel characters |
| **4. New selective pressures** | | |
| a. Natural | | Novel characters |
| b. Human | | Novel characters and novel combinations of characters |

### 3.2.1. First scenario: rapid expansion

A rapid expansion of barley in Ethiopia seems to have been the causal factor behind an explosion of varieties in Ethiopian barley. The large diversity of novel forms (*e.g.*, the forms *deficiens* and *irregulare*) endemic to Ethiopia confused Vavilov and led him to originally consider Ethiopia as barley's primary centre of domestication[9] (Vavilov 1926). Population increase after a bottleneck seems also a plausible explanation for the diversity of bananas in the region of the Great Lakes in Africa, although an accumulation of somatic mutations could have amplified the phenomenon (Pickersgill 1998).

### 3.2.2. Second scenario: repeated introductions

Independent, multiple introductions can also contribute to mitigate the bottleneck effect, by increasing in size the subset of genetic diversity sampled from the area of origin and introduced to the new area. The impressive diversity of beans in East Africa (Martin & Adams 1987a,b, Pickersgill 1998) and watermelons in Brazil (Romão 2000) probably resulted from such spatial compression of diversity. Beans were probably introduced independently at least twice to Africa, from different source areas, resulting in the occurrence together, within the scale of a single African field, of types of beans otherwise found only in Mesoamerica or the Andes, but never together.

[9] Barley, in fact, was domesticated in the Fertile Crescent (Zohary & Hopf 1994).

A similar scenario for manioc in Africa is supported by the high genetic diversity that may be found locally in African manioc farms (Lefèvre & Charrier 1993). Manioc was introduced into Africa several times, first, in the 16th century, in São Tomé, Congo, and West Africa, and then, in the 18th century, from East Africa (Jones 1959). Exactly how many times manioc was introduced, and how many varieties were introduced into Africa, is not known, but given the technical difficulty at the time of transporting manioc stem cuttings overseas, the Portuguese most likely selected a large range of local landraces in order to evaluate them in their African colonies (Pickersgill 1998). As in the case of the watermelon, spatial compression of diversity could have occurred in these areas where the Portuguese were particularly active in the 16th and 17th centuries, *e.g.*, on Fernando Pó (now Bioko), on the islands of São Tomé and Príncipe, in Sierra Leone, or around Luanda and the mouth of the Congo River (Jones 1959).

### 3.2.3. Third scenario: hybridization

If repeated introductions occur within the same, geographically restricted area, this will locally produce a hotspot of diversity, but it will not necessarily imply *de novo* creation of diversity. Local concentration of diversity can result from farmers' active compilation of phenotypically contrasted forms (see for example Boster 1984a, Elias *et al.* 2000a, Delêtre & McKey submitted). However, diversity is, in this case, allochthogenous (*sensu* Mayr 1937). I propose to term such hotspots *passive hotspots* of diversity. By opposition, *active hotspots* are localized areas in which diversity is created, not just accumulated. In this respect, the conscious or unconscious selection (Zohary 2004) by local farmers of crop volunteer seedlings, which result from the recombination and segregation of characters through sexual reproduction, is determinant.

Hybridization can occur between genetically diversified types of a crop, isolated in the crop's original range but put into situations of sympatry in the new area, magnifying local diversity in the area of introduction. Although limited in the case of bean, where crosses between the Mesoamerican and the Andean types were hindered by genetic barriers, hybridization between diversified types is the most likely source of the high variation found within varieties of watermelon in Brazil, and the probable source of most of the variation found in African manioc (Pickersgill 1998).

Watermelon is a crop indigenous to Africa. Throughout the slave trade period (16th-19th centuries), watermelon was introduced to Brazil several times by African slaves, deported to the Portuguese colonies in north-eastern Brazil to work on sugarcane

plantations. Occurrence within slaves' gardens of a large diversity of strains of watermelon favoured hybridization between highly differentiated varieties, resulting in an explosion of watermelon diversity in north-eastern Brazil (Romão 2000). Gene flow between the different manioc types could have similarly favoured the appearance of new combinations of characters where manioc was repeatedly introduced, and contributed to enlarge the genetic base of manioc in Africa (Pickersgill 1998).

Hybridization with wild relatives present in the area of introduction can also contribute to generate diversity, and could even favour the appearance of new characters hitherto unknown in the area of origin (Pickersgill 1998). Spontaneous hybrids of manioc with Ceara rubber tree (*Manihot glaziovii* Muell.-Arg.), another species of the genus *Manihot* introduced into Africa around 1900 (Jones 1959), have been reported in Madagascar (Cours 1951) and Côte d'Ivoire (Lefèvre & Charrier 1993).

### 3.2.4. Fourth scenario: changes in selective pressures

Finally, local adaptations (the allochthogenous sources of diversity, *sensu* Mayr) could also have contributed to amplify manioc genetic diversity in Africa, as in the case of sweet potato (Gichuki *et al.* 2003). The changes in selective pressures between a crop's area of origin and its areas of introduction are another mechanism that can explain the emergence of secondary centres of diversity. Where human selection is concerned, how these new pressures of selection orient the evolution of secondary centres of diversity is however highly dependent on the relation that the people have formed with the new crop.

## 3.3. Men, plants, and ideas

All these different scenarios stress the importance that sexual reproduction could have played in the diversification of manioc in Africa. Farmers, through their perception of manioc biology and attitude towards diversity, have therefore been the main actors of the secondary diversification of manioc in Africa.

Despite their importance for genetic diversity at the local scale and their probable role in evolving a secondary centre of diversity for manioc in Africa (Lefèvre & Charrier 1993, Pickersgill 1998, Fregene *et al.* 2003), the patterns of folk biological reasoning with respect to the management of manioc volunteers in African farming settings have been little investigated. Current evidence suggests that farmers' knowledge about manioc volunteers is overall less developed and less widespread in Africa than in Amazonia (McKey *et al.* 2001), but also very heterogeneous across communities, and even among

farmers within a single village (*e.g.*, de Waal *et al.* 1997, Mkumbira *et al.* 2003, Manu-Aduening *et al.* 2005, Kizito *et al.* 2007a). Other crops suggest a similar situation, and African farmers show generally little interest for the volunteer seedlings of sweet potato (Gibson *et al.* 2000), another vegetatively propagated plant of neotropical origin introduced into Africa in the 16$^{th}$ century (O'Brien 1972). Paradoxically, in West Africa, farmers seem to readily make use of yam volunteer seedlings as a source of potential diversity (Scarcelli *et al.* 2006). The domestication of yam (*D. cayenensis* Lam., *D. rotundata* Poir. complex) through the use of yam volunteers is still an active process in West Africa (Dumont *et al.* 2006, Scarcelli *et al.* 2006).

### 3.3.1. Evolution and devolution of folk ecological knowledge

When manioc was introduced into Africa, the knowledge that the Portuguese transmitted to Africans about manioc cultivation and processing techniques was only partial. In Brazil, the Portuguese learned manioc cultivation and preparation from the Tupinambá Amerindians (Jones 1957). The Portuguese later only transmitted their own, incomplete knowledge of Amerindian techniques to the Africans. Among the elements of know-how which were lost along this chain of cultural transmission was Amerindian basketry techniques and the making of the manioc sleeve press, the **tipiti**, which the Tupinambá and many other Amerindian societies use to detoxify bitter manioc, but which the Portuguese did not learn how to make (Jones 1957).

In the domain of manioc processing, Africans innovated. By adapting methods traditionally used for wild toxic yams (Jones 1959), Africans invented new ways to detoxify and prepare manioc (Lancaster *et al.* 1982). The sets of technical innovations surrounding manioc processing in Africa underwent several successive modifications, until African techniques had become completely different from the original Amerindian techniques, which the Africans never witnessed.

This acculturation process led to several new forms of preparing manioc, which are typically African ways (Lancaster *et al.* 1982). Manioc *bâtons*, also known as **chikwangue** in Congo, for example, are genuine African inventions. The same situation probably held true for farming techniques. The Portuguese had taught Africans how to plant manioc through cuttings—or Africans learned from observing manioc plantations around Portuguese forts—but Amerindian farmers' folk ecological knowledge about volunteer seedlings was not passed onto African farmers. It had to be re-invented.

### 3.3.2. Cultural domestication

In the crop areas of introduction, secondary centres have evolved from the re-appropriation of the plant by local populations, through a process of acculturation which has enriched both the plants and the people themselves. Compared to Amerindian farmers, who domesticated the crop over millennia, African farmers have had much less time to 'domesticate' manioc, this time in a cultural sense. Richards (1985) however defined African farmers' "inventive self-reliance" as their most precious resource. Because their folk biological knowledge about indigenous crops may have produced some "habits of mind" (Ross & Medin 2005), farmers could have transposed to manioc the knowledge they already acquired while managing similar indigenous plants, such as yams (see Scarcelli *et al.* 2006).

Slowly 'domesticating' the newly introduced plants, African farmers developed their own experience of manioc cultivation, and made it either a minor part or the mainstay of their agriculture and lifestyle. The extent to which sexual reproduction contributed to maintaining, or possibly even increasing, manioc genetic diversity in Africa has depended on the processes through which African farmers built their own folk ecological knowledge of the crop. To date, however, nothing appears to be known about the 'roots' of this process of cultural domestication, and its role in the secondary diversification of manioc in Africa.

# 4. Unravelling the dynamics of manioc diversity in Africa

## 4.1. Aims of the study

The general focus of this thesis is the study of the role of plant-farmer interactions in the dynamics of manioc diversity in Africa. This question was explored through a series of village-level studies of traditional manioc farming systems in Gabon, Central Africa, as a model study for investigating the mechanisms underlying the secondary diversification of manioc in Africa. The aim of this thesis is the identification of the grounds (social, cultural, economic or historical) of farmers' perception and valuation of diversity, and the documentation of their consequences for manioc genetic diversity.

## 4.2. Outline of the thesis

In Chapter II, I first tackle manioc diversity in its broad sense definition, and present the methodological approach I followed to study cross-cultural variations in the perception, valuation, and management of diversity. The specific aims of this chapter are:

1. To characterize the geographical patterns of manioc diversity in Gabon;
2. To identify and target areas for in-depth studies of the processes that shaped the patterns of diversity in Gabon.

In the next three chapters (III, IV, and V), I contemplate diversity at the community level, in three case studies of traditional manioc farming systems in Gabon. Each chapter addresses a set of specific questions identified in Chapter II, and starts with a brief introduction into the history of the communities studied. I then describe the farming systems in which manioc is embedded, based on my own field observations and complemented by literature when available.

Using a population genetic approach to investigate the biological dimension of local folk taxonomies of manioc landraces, I examine folk nomenclature systems and analyze the structure of manioc genetic diversity at the community level. Finally, I discuss the relationship between farming practices and genetic diversity, aiming to demonstrate the active role, conscious or unconscious, of farmers in managing manioc genetic diversity at the local level.

Leaning my argumentation on these three case studies, I show how intricate is the history of the plant with that of people, and how this historical 'co-evolution' has been a particularly important dynamic in shaping the heterogeneous patterns of manioc diversity in Gabon. The specific aims of these chapters are:

1. To review the diversity of manioc farming systems in Gabon;
2. To identify the cultural and historical factors that have built up or influenced the patterns of manioc genetic diversity in Gabon.

From the diversity of farming practices I have documented in Chapters III, IV and V, I summarize in Chapter VI the general findings from the three case studies of manioc farming systems, and reintegrate the notion of landrace into a more theoretical framework, to comprehend the role of farmer-plant interactions on the dynamics of manioc genetic diversity. I finally discuss the importance of the pluridisciplinary approach I followed to understand the dynamics of genetic diversity in vegetatively propagated crops in their areas of introduction, and suggest some directions for future studies of manioc genetic diversity in Africa.


**Plate II**

**Manioc reproductive biology**. Manioc inflorescences, showing (a) young male (pistillate) manioc inflorescences and (b) mature female (staminate) flowers. Manioc is pollinated by insects (meliponins). Female flowers develop before male flowers to avoid self-pollination.


**Plate II** (continued)

**Manioc reproductive biology**. Mature manioc fruits (c). Fruit maturation occurs 75-90 days after pollination. Seeds are dispersed by explosive dehiscence (d), and can remain dormant for several decades. In traditional shifting cultivation systems, the increase in soil temperature following removal of vegetation breaks seeds dormancy, and seedlings (e) appear within two weeks following burning.

# Chapter II

## *Mingling disciplines*
## *to untangle the patterns of diversity*

## Notes

1. For stylistic convenience, I have adopted a simplified version of the official Gabonese spelling for the names of ethnic groups* (Carpentier de Changy & Voltz 1990), which also differs from the traditional semi-phonetic spelling employed by Guthrie (1948). The phonetic sounds [ɛ], [ɔ] and [ŋ] are written è, o and ng, while [ɣ], [ʃ] and [β] were written gh, sh and vh, respectively.
2. Ethnic groups are identified by their language, denoted after Maho's (2003) proposed revision of Guthrie's classification of Bantu languages.
3. Topographic names I used are those of the official map of Gabon: carte au 1:1,000,000 (INC 1994) from the INC (Institut National de Cartographie, Libreville) and IGN (Institut Géographique National, Paris).
4. Landraces names are indicated in italics, using single quotes (‘’) following the standard orthography of cultivar epithets in accordance with the International Code of Nomenclature for Cultivated Plants (Brickell 2004).

# 1. The current knowledge on manioc genetic diversity

Started by colonial authorities in Africa ca. 1910 (Jones 1959), research for improving manioc agriculture through plant breeding is carried out by several institutions, such as IITA[10] in Nigeria and CIAT[11] in Colombia. Both have undertaken, since the 1960s, to sample and evaluate manioc genetic diversity (Jennings & Iglesias 2002).

A crop's gene pool (*sensu* Harlan & De Wet 1971) is the genetic reservoir upon which modern breeding can draw to select new traits (*e.g.*, disease resistance). With 6,000 accessions, CIAT holds the largest *ex situ* collection of manioc accessions. IITA, which has a mandate for African germplasm, holds approximately 2,500 accessions (FAO 1998). However, an estimated 65% of the manioc gene pool still remains to be collected (Fowler & Hodgkin 2004). Only 37% of all landraces have been collected, and only 5% of wild species have been sampled (FAO 1998).

Primary centres of manioc diversity have been identified as three regions of South America, one that encompasses eastern and southern regions of Brazil, along with Paraguay, another that covers southern Venezuela, eastern Colombia and northern Brazil, and a third one that extends from Nicaragua to Panama and Honduras (Raffaillac & Second 2001). Several areas are also recognized as secondary areas of diversification, *e.g.*, Bolivia, the Amazon basin, north-eastern Brazil, southern Mexico, and Africa (Lefèvre & Charrier 1993, Pickersgill 1998), where greatest diversity is found in Central and West Africa (Gulick *et al.* 1983).

## 1.1. The puzzle of manioc diversity in Africa

Many authors agree on the tremendous diversity of African manioc (Lefèvre & Charrier 1993, Pickersgill 1998, Fregene *et al.* 2003, Mkumbira *et al.* 2003, Manu-Aduening *et al.* 2005, Kizito *et al.* 2005, 2007), but the extent of this diversity—as well as its nature—remains to date quite ambiguous. Manioc diversity in Africa appears to be quite variable, depending on the scale of the study. Variations of high magnitude have been found at the regional level (Fregene *et al.* 2003), but also at the village level.

[10] International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria.

[11] Centro Internacional de Agricultura Tropical (CIAT), Cali, Colombia.

Depending on studies, the number of landraces found at the village level varied between 4 and 23 in Cameroon (Dounias 1993), 15 and 50 in Malawi (Chiwona-Karltun *et al.* 2000, Mkumbira *et al.* 2003), and 1 and 20 in Uganda (Otim-Nape *et al.* 2001). Previous studies have not attempted to investigate the source of these variations. Yet, in addition to the necessity of evaluating local genetic resources, it is also necessary to understand how diversity is structured in space, and how it evolves in time.

## 1.2. A call for data

While several surveys focusing on local management of diversity at the village level have been conducted in Amazonia (Salick *et al*. 1997, Emperaire *et al.* 1998, Elias *et al.* 2000a, Duputié *et al.* 2009b), similar studies are still scarce in Africa (*e.g.*, Mkumbira *et al.* 2003, Manu-Aduening *et al.* 2005, Kizito *et al.* 2007). African figures suggest nevertheless that there is considerable diversity (Mkumbira *et al.* 2003, Kizito *et al.* 2005, 2007) but also considerable heterogeneity in levels of genetic diversity in African manioc (Fregene *et al.* 2003). With regard to the diversity of the African continent, so few sites have been studied that it is however impossible to know whether this heterogeneity in Africa reflects the past history of the crop's introduction and diffusion into the continent (various founder effects), socioeconomic factors that differently affected farmers' decision to grow small or large numbers of landraces, or cultural differences, which stem from reasons no discipline but anthropology can account for.

A number of reviews have stressed the extent to which African people, while adapting their farming systems or inventing new ones, have developed their own experience of manioc farming (Fresco 1986, Richards 1985). Africa's complex history and multiplicity of cultures must have played a major part in shaping the high diversity of manioc in Africa, and cultural diversity probably accounts for a large part of the strong regional disparities in varietal richness of manioc. Most likely the present picture of diversity is the outcome of a combination of different factors, but determining their relative contributions is essential to understand the dynamics that shaped diversity at the local and regional levels.

It requires approaching the different landscape variables that impinge on crop diversity, including agroecological factors, demographic pressures, and regional socioeconomic constraints likely to affect the organisation of the farming systems. In this chapter, I present the methodological approach I used to characterize manioc diversity in Gabon, and the sequential approach I used to investigate the origin of this diversity.

# 2. Solving the complex nature of manioc genetic diversity

Manioc diversity, in the broad sense, can be comprehended at different levels, from that of the landrace to that of the entire region (Fresco 1986, McKey *et al*. 2001). Each level is pertinent, and allows the exploration of a different set of questions. The perception of diversity is thus strongly dependent on the scale of observation (Emperaire *et al.* 1998, Pinton 2003), and understanding the dynamics of diversity requires spanning all the different levels.

To depict and decrypt the patterns of manioc diversity in Gabon, I followed a systemic approach (Figure 2.1) that combined ethnobotanical surveys of local farming systems and population genetic studies to investigate folk nomenclature systems of manioc landraces.

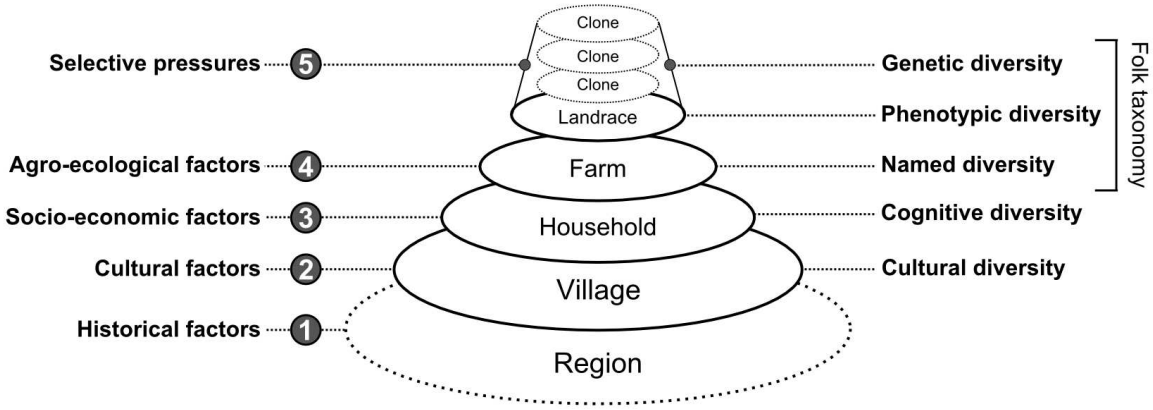



**Figure 2.1. A systemic approach to manioc diversity** (adapted from Fresco 1986). Cultural diversity refers to differences between societies in knowledge and categorization of diversity, while cognitive diversity designates differences between individuals (*i.e.*, idiosyncrasies). Because named diversity* and phenotypic diversity do not always match (the former being the result of the perception of the latter), a distinction was made between the two levels. The landrace was represented as an ensemble of clones.

Manioc diversity was approached through a series of village-level studies of traditional manioc farming systems in Gabon. I first examined manioc diversity at the regional level, to characterize the general patterns of manioc diversity (this chapter). I then focussed on the community level, where cultural factors could be approached. The third level I considered was the household, where socioeconomic constraints apply. The fourth level, the field, allowed me to assess agro-ecological (natural and anthropogenic) factors that interact with manioc populations. The landrace, the smallest folk taxonomic unit on which farmers exert selection, was the last level of the study, at which genetic diversity was finally assessed, and the consistency of nomenclature systems was evaluated.

## 2.1. Study area

The study was carried out in Gabon, Central Africa. Located in the Gulf of Guinea, and lying between 2°15'N and 4°S latitude, and 8°30' and 14° E longitude, Gabon is bounded by Equatorial Guinea and Cameroon to the north, and by Congo to the east and south. Gabon is home to approximately 50 different Bantu tribes* (Appendix A1), for a total population of just about 1.5 million inhabitants (World Bank 2009). The Fang [A.75] represent about one-third of the population (ca. 600,000). Punu ([B.43], ca. 143,000), Ndzabi ([B.52], ca. 124,000), Myènè ([B.11], ca. 56,000), Ghisir ([B.41], ca. 47,000) and Tsogho ([B.31], ca. 30,000) represent the five other principal ethnic groups* (Lewis 2009). Gabon however counts numerous other tribes, including a small Pygmy population (totalling ca. 5,000).

Gabon is sparsely populated. Population density is low overall (average 4.7 inhabitants $\times$ km$^{-2}$), and very unevenly distributed across the country, with high population concentrations around urban agglomerations (Libreville, Port-Gentil, Franceville, Bitam). The rural population, in contrast, represents only 20% of the total population, leaving large depleted areas where population density ranges between 0.5 and 1.7 inhabitants $\times$ km$^{-2}$ (Appendix A3). Despite being rather uniform in its vegetation cover—nearly 85% of the territory (267,667 km²) is covered with equatorial forest—Gabon also has small areas that differ in their ecological and climatic conditions (Appendix A4). Cultivated areas represent less than 1% of the territory (FAO 2008).

Gabon has one of the highest *per capita* GDP (Gross Domestic Product) among sub-Saharan African countries (5,500 EUR in 2007 according to the World Bank). Yet, about two-thirds of the population still lives below the national poverty line (FAO 2008), and Gabon ranks 119 in the Human Development Index (World Bank 2009). Oil and timber industries represent most of the country's exportations, and account for 57% of Gabon's GDP (FAO 2008). The agricultural sector, conversely, is marginalised, and represents only 5% of the country's revenue.

Swidden agriculture farming systems are predominant in Gabon. Farmers practice slash-and-burn cultivation, with intervening fallows. Polyculture, involving crop rotation and intercropping (*i.e.*, the association of different crops in the same field) is prevalent. Manioc, plantain, yam, taro, peanut and sugarcane are the most important crops.

In 2007, the country produced about 275,000 tons of plantains and about 240,000 tons of manioc (FAO 2009). However, lack of appropriate infrastructures has been a curb to the prospect of developing opportunities for the commercialization of farming products (FAO 2008). Isolation of villages, the cost of transport and problems of storage have impeded the transformation of local farming into an economically viable activity.

Since decolonization in 1960, Gabon has concentrated efforts on developing oil and timber industries to the detriment of agriculture, with, as a result, a decrease by 42% of the rural population, and by 51% of the total cultivated area (FAO 2008). Created in 1975, the Centre d'Introduction, d'Adaptation et de Multiplication du Matériel Végétal, Fruitier et Maraîcher (abbreviated CIAM), based in N'toum, has a mission to enhance agriculture by favouring farmers' access to a larger choice of improved seeds. The centre currently holds approximately 60 IITA cultivars of manioc in field genebanks (FAO 1998). However, the CIAM and its satellites in Booué, Lambaréné, Oyem and Tchibanga, have all virtually stopped their activities since the 1990s because of lack of sufficient investment to maintain the collections (FAO 2008). Agriculture in Gabon is therefore essentially confined to subsistence, and food importations cover about 60% of the country's agricultural needs (FAO 2008).

### 2.1.1. Study sites

The comparative study I carried out on the diversity of manioc farming systems in Gabon covered ten communities, which together represent a large span of the country's ethnic and natural diversity (see Appendix A). The ten villages were chosen to present marked cultural, agroecological and socio-economic contrasts.

In each village, I spent between two and three weeks studying the organization of the farming system, drawing inventories of varietal diversity, and recording farmers' statements, practices and perceptions regarding manioc volunteers. Fieldwork was spread over two periods of four months, from mid-August to mid-December, in 2006 and 2007. I targeted the transition between the dry and rainy seasons, a period corresponding to the time farmers weed and plant their new farms, and where most manioc volunteers appear.

### 2.1.2. Survey of the farming system

The number of interviews in each village was set to a minimum of 15 and a maximum of 30, which are standard survey sizes in the literature (see Elias *et al.* 2001b, Manu-Aduening *et al.* 2005, Mkumbira *et al.* 2003). I used rarefaction curves to determine the minimum number of persons interviewed required to ensure that the sample size was appropriate to appraise all named diversity present at the village level[12].

Informants were randomly selected amidst farmers willing to participate. Age, village of birth, and parental lineages were recorded for each farmer (Appendix B1). Because it was important that the sample covered the whole community, but also avoided biases associated with the frequent organization of villages into districts of relatives, I drew maps of each village (Appendix B2), on which districts and the location of my informants' houses were reported. In addition, social networks describing farmer kinship relations and links to working groups were drawn for the subset of farmers interviewed (Appendix B3). In order to 'weight' information appropriately and not to make a general rule of idiosyncratic beliefs and practices, I only considered information that had been confirmed independently by at least two farmers.

All interviews were conducted independently, during visits of the farms in the company of their owners, and in the presence of an interpreter, to help with the transcription and translation of vernacular names. The organization of the farming systems was explored through semi-directive interviews, structured into five major themes: (i) land management (rules of appropriation of land and fallow), (ii) agricultural calendar (timing of clearing, burning, planting and harvesting), (iii) intercropping (distribution of crops in time and space), (iv) weeding and (v) pest management (identification of local pests and diseases). Farmers were also questioned about their folk ecological knowledge, in particular about manioc reproductive biology (flowers, fruits, and seeds) and criteria of selection of cuttings.

To study exchange networks of cuttings I asked farmers when, how and/or from whom they obtained the landraces they grow. Manioc processing techniques and other materials were collected during open discussions in the village.

[12] The rarefaction curve approach consists in plotting the increase in total number of landraces inventoried with the increasing number of farmers interviewed. The minimum size of the sample is determined by the shape of the curve. As long as a plateau is not reached, it is necessary to increase the sample size.

## 2.2. A multidisciplinary approach to manioc diversity

The methodology I followed, combining ethnobotany with population genetics, made possible the study of the genetic variation caused by farmers' interaction with manioc biological traits, through the way they perceive diversity, manage it, use it, and select upon it.

Ethnobotany is the study of the folk botanical knowledge associated with the perception, organization and management of the diversity of plants (Berlin 1973). Folk taxonomy describes the local system of classification, naming, and identification of the diversity of types found within a crop (Berlin 1973). The function of folk biological classification of diversity into discrete units—the landraces—is to permit the socialization of diversity, which allows landraces to be managed and exchanged between farmers (Friedberg 1986, Boster 1986), within and between communities. Friedberg (1986) decomposed the process of classification into three steps:

1. Identifying diversity, *i.e.*, recognizing differences between the types;
2. Denominating diversity, *i.e.*, labelling variants by attributing them a name;
3. Socializing diversity, by inserting it into a common system of references.

To study folk taxonomic systems and understand the role of farmers as the main actors of the evolution of crops' genetic diversity, I based my methodology on Harlan's definition of the landraces (see Chapter I), and explored the named, morphological and genetic dimensions of manioc diversity.

### 2.2.1. Assessing named diversity

In their farms, I asked farmers to name all manioc landraces they could recall from memory. To characterize the distribution of named diversity at the village level, two indexes of evenness adapted from Heip (1974), $E_v$ and $E_f$ ($v$ standing for variety and $f$ for farmer), were calculated:

$$E = \left(e^{H'} - 1\right)/\left(L - 1\right) \qquad [1]$$

where

$$H' = -\sum p_i \ln p_i \qquad [2]$$

In the case of $E_v$ and $E_f$ respectively, $L$ represents the total number of landraces and the total number of farmers. $p_i$ represents ($E_v$) the proportion of farmers growing the landrace $i$, and ($E_f$) the proportion of landraces owned by the farmer $i$. When $H'$ decreases, $E$ tends to 0. $E_v = 1$ when all landraces have the same frequency among farmers. $E_f = 1$ when all farmers have the same number of landraces.

### 2.2.2. Assessing morphological diversity

Phenotypic diversity is the base of the classificatory process, and can be decomposed principally in three sets of criteria, listed by Shigeta (1996) as follows:

1. The outer morphological characteristics, immediately perceptible (*e.g.*, leaf colour, stem colour);
2. The agronomic characteristics, which are learned only after a period of observation (*e.g.*, life-cycle);
3. The organoleptic characteristics, which are associated with particular uses of a given landrace (*e.g.*, taste, and whether the landrace is considered "bitter" or "sweet").

When interviewing farmers, I asked them to elicit all parts of the plant they look at when identifying a landrace, and also collected other passport information, such as yield, bitterness, or organoleptic characteristics of landraces (taste, colour, processability). In addition, I assessed morphological diversity using a synthetic list of descriptors, based on the morphological keys proposed by Cours (1951), Rogers and Fleming (1973), Second *et al.* (1999) and Emperaire *et al.* (2003). Thirty morphological descriptors were used to describe landraces:

1. Leaf: general colour of young leaves and mature leaves, colour of the leaf veins (upper and lower surface) on both young and mature leaves, number of lobes and their shape (length/width ratio), length and colour pattern (basalmost extremity, first third, second third, last third, and distalmost extremity) of the petiole.
2. Stem: length, diameter, degree of ramification, angle of the first ramification, colour of the epidermis and of the cortex, protuberance (measured in mm) and density (number of leaf scars on 30 cm of stem) of the leaf scars, and length of internodes (in cm).
3. Root: surface texture, colour of the epidermis, colour of the inner peel, and colour of the pulp (it was also recorded whether the landrace is 'bitter' or 'sweet' as categorized by farmers, however the actual cyanogenic potential of roots was not measured).
4. Flower: presence/absence, colour of the torus.

### *The trouble with manioc*

Studying the morphological diversity of manioc poses a methodological difficulty. The trouble with manioc is that morphological characters change as the plant ages. Morphological characteristics of the manioc plant, including many of the most commonly used descriptors, such as the number of lobes of the leaf (Cours 1951) or the colour of the petiole (Boster 1985, Sambatti *et al.* 2001, Kizito *et al.* 2007), vary over the growth of the plant (Raffaillac & Second 2001). Manioc leaves are heteroblastic: on the same plant, leaves may display a large range of variations for the number of lobes (usually, a top-down increase in the number of lobes). Additionally, other morphological traits, such as the plant's architecture (degree of branching, frequency of reiteration), are affected not only by genetic differences but also by the environment, varying for example with the composition of soil (Raffaillac & Second 2001).

Given the plasticity of morphological traits in the manioc plant, measuring phenotypic diversity is problematic, and several authors have underlined the weakness and inadequacy of morphological keys (Raffaillac & Second 2001, Chiwona-Karltun *et al.* 1998, Elias *et al.* 2001a, Emperaire *et al.* 2003, Mkumbira *et al.* 2003, Manusset 2006). As Shigeta (1996) stressed in the case of ensete, confirming a synonymy between folk landraces from distant locations is therefore practically impossible on the sole basis of a comparison of their morphological characteristics, and it is therefore necessary that a morphological approach be coupled with a genetic approach to diversity (McKey *et al.* 2001, Manusset 2006, Kizito *et al.* 2007).

In this thesis, I favoured the genetic approach to diversity, and morphological diversity was only assessed to bring support to the genetic data. To appraise agreement in folk taxonomies, I examined the "genetic integrity" of landraces (see Harlan's definition) using an *a posteriori* method, based on the analysis of the mismatch between the "cultural" and the "natural" (*sensu* Manusset 2006) definition of a landrace, that is, on the evaluation of the consensus among farmers in their classification of manioc landraces into biologically meaningful entities, through an evaluation of the genotypic composition of landraces.

### 2.2.3. Assessing genetic diversity

In order to obtain a comprehensive assessment of genetic diversity, I used a stratified sampling method. Following farmers' indications, I collected five samples per landrace per farmer from randomly selected plants. The sample size thus reflects the popularity of the landraces (*i.e.*, their frequency amongst farmers). Because manioc landraces are often planted in small monovarietal patches, the closer the individuals, the higher the probability that they are clonemates. The five sampled plants were therefore chosen to cover the whole distribution range of the landrace in the field, each one distant from the others, to avoid any bias and risk of underestimating the rate of polyclonality in manioc landraces. Leaves were enclosed in envelopes labelled with the name of the landrace and its origin (owner and field), then dried within hours following collection and stored with silica gel.

Since the advent of molecular biology in the 1980s, several kinds of markers have been developed for screening and characterizing genetic diversity. Genetic markers are heritable characters (loci), each of which can take one or several states (alleles). In diploid organisms, the same individual can have two copies of the same allele (homozygous) or have two different alleles (heterozygous). Allozymes, randomly amplified polymorphic DNA (RAPD), restriction and amplified fragment length polymorphic DNA (RFLP and AFLP), simple sequence repeats (SSR) and single nucleotide polymorphism (SNP) are now available for unveiling the patterns of genetic diversity. Sunnucks (2000) categorized the different techniques in two groups: the multilocus approaches (RAPD, AFLP, RFLP), where several random characters are screened simultaneously, and the single-locus approaches (allozymes, SSR, SNP), which target several specific loci.

*Different markers for different questions*

Robinson and Harris (1999) and Sunnucks (2000) have discussed the advantages and disadvantages of both approaches. There are three particularly important criteria to consider for choosing the most appropriate marker: 1) sensitivity, *i.e.*, the marker must detect enough variation for allowing fingerprinting of genetic diversity, but must also not obscure patterns of diversity by yielding too much information, 2) connectibility, *i.e.*, the marker must allow the comparison of results from several independent studies, and 3) neutrality. Particularly when studying evolutionary processes, the marker must not be directly subject to selection.

Simple sequence repeats (SSR), also known as microsatellites, are short stretches of tandem repeats of nucleotide sequences, generally less than five base pairs (bp) in length. Microsatellites are non-coding regions found in all eukaryotic genomes. They are hypervariable[13], and like AFLP, they can reveal a large amount of polymorphism (Robinson & Harris 1999). Changes in the length of microsatellite regions, *i.e.*, variations in the number of tandem repeats, occur when the DNA polymerase 'slips' while replicating DNA. Assaying these length variations (henceforth termed 'alleles') allows detecting variability within closely related populations, at both inter- and intraspecific levels species.

### *The advantages of microsatellite markers*

Microsatellites, unlike RAPD and AFLP markers, are co-dominant (*i.e.*, both alleles contribute to the phenotype[14]) and therefore better suited for population genetics, where information on the heterozygous state of individuals is essential for the characterization of genetic diversity and the elucidation of mating systems, parentage and other variables. Another major drawback of the AFLP/RAPD multilocus approach is the only limited comparability of the results among studies (Sunnucks 2000). Partial digestion of DNA, in particular, is an important source of artefactual polymorphism that reduces connectibility of results across studies (Robinson & Harris 1999, Sunnucks 2000). Microsatellites, in contrast, provide robust and reproducible data. They also have higher resolving power, and require smaller sample size than do SNP (Kawuki *et al.* 2009) or AFLP (Robinson & Harris 1999) markers to achieve similar analytical power.

Many SSR markers have been developed for cultivated manioc (Chavarriaga-Aguire *et al.* 1998, Mba *et al.* 2001, Fregene *et al.* 2003) and in recent studies of manioc genetic diversity (*e.g.*, Elias *et al.* 2001a, Mkumbira *et al.* 2003, Elias *et al.* 2004, Kizito *et al.* 2005,2007, Sardos *et al.* 2008, Duputié *et al.* 2009b), microsatellite markers have been preferred to other markers, such as allozymes (Sambatti *et al.* 2001, da Silva *et al.* 2003), RAPD (Asante & Offei 2003), AFLP (Elias *et al.* 2000b, Fregene *et al.* 2000) and SNP (Olsen 2004, Kawuki *et al.* 2009).

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[13] Mutation rate at microsatellite loci is estimated to be around $10^{-5}$-$10^{-2}$ per base per generation (Jarne & Lagoda 1996), but varies between microsatellite loci. The repeat motif and especially the number of repeats seem to have the major effect on the mutation rate of microsatellites (Kruglyak *et al.* 1998).

[14] Both alleles present at a locus are expressed and can be scored, enabling distinguishing between homozygous (AA, aa) and heterozygous (Aa) states.

The genetic diversity of manioc in Gabon was assessed using ten neutral nuclear (biparentally inherited DNA) microsatellite markers[15] [GAGG5, GA12, GA21, GA57, GA126, GA134 (Chavarriaga-Aguirre *et al.* 1998) and SSR31, SSR55, SSR68, SSR169 (Mba *et al.* 2001)], with broad coverage of the genome and widely used in similar studies of manioc genetic diversity (Elias *et al.* 2001a, Narváez-Trujillo *et al.* 2001, Olsen & Schaal 2001, Fregene *et al.* 2003, Mkumbira *et al.* 2003, Elias *et al.* 2004, Olsen 2004, Kizito *et al.* 2005, Pujol *et al.* 2005b, Lokko *et al.* 2006, Pujol & McKey 2006, Duputié *et al.* 2009a,b).

For each village, only a sub-sample of the sample collected was analyzed. The rule of thumb I followed in selecting samples was to maximize both the number of farmers and the number of landraces included in the data set. In addition, farmers were selected in such a way that those included in the data set shared the greatest number of landraces, so as to maximize the number of possible comparisons between farmers, on which the analysis of folk taxonomy systems of manioc landraces depended (see below). Genetic analyses followed the methodology described in Appendix C1.

### 2.2.4. Delving into folk taxonomy

At the community level, landraces are recognized through a common name. The basis of the local taxonomy of landraces is therefore lexical, and only partially shared between farmers. At the individual level, the perception and categorization of phenotypic diversity into pertinent entities is first and foremost a personal experience, and names given to landraces are only there to permit exchange, but do not necessarily imply that all farmers will designate the same clone (or set of clones) under the same name. This particular dimension of diversity, cognitive diversity (Boster 1986), was investigated through a study of consensus between different farmers' taxonomies of landraces.

Consistency of identifications amongst farmers was explored through an analysis of the genotypic structure of manioc landraces[16]. All plants with complete genotype (no missing allele) were first sorted according to their multilocus genotype (MLG), independently of local folk taxonomy. A group (*viz.*, a set of clonemates) was defined whenever more than one copy of a given MLG was found in the data set.

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[15] More details on primers can be found in Table C1.2 in Appendix C1.

[16] This approach rests on the assumption that the set of molecular markers used for the genetic analyses allowed for an accurate description of the genetic diversity (sufficient resolving power, see Appendix C2).

MLGs were categorized as follows:

1. Whenever the majority ($\geq 50\%$) of plants showing a given MLG belonged to the same landrace, the MLG was said to be typical of the landrace;
2. If all plants showing a given MLG belonged to the same named category, then the MLG was said to be specific to the landrace;
3. Sometimes, the same MLG was typical of several named landraces, indicating a case of synonymy. The MLG was then said to be shared between the different landraces;
4. Groups consisting of admixtures of one, two or three plants assigned to various landraces, with none accounting for the majority, were considered as non-typical.
5. Singletons *i.e.*, individuals with a genotype not shared with any other individual, were considered as 'atypical'.

Whenever there was mismatch between a plant's genotypic membership and its named category, *i.e.*, when the plant was said to belong to a landrace but displayed a MLG typical of another one, the plant was considered as 'mislabelled'.

Based on the above categorization of MLGs, I applied Boster's index of agreement, $OA_j$ (Boster 1985a), to evaluate the consistency of identification of the most common landraces amongst farmers. Scoring the number of times farmers agreed in assigning a given genotype to a landrace, I first calculated $PA_i$, the proportion of agreement for the informants pair $i$, as follows:

$$PA_i = \frac{a_i}{n_i} \qquad [3]$$

where $a_i$ is the number of times the pair $i$ agrees and $n_i$ the number of comparisons. $OA_j$ derives from $PA_i$, and gives the overall agreement between between informant $j$ and all other informants:

$$OA_j = \sum PA_{ji} \Big/ n_j \qquad [4]$$

where $PA_{ji}$ is the proportion of agreement between farmer $j$ and any other informant $i$, and $n_j$ is the number of comparisons involving farmer $j$. By convention, $OA_j$ was calculated for $n_j \geq 10$ only.

### 2.2.5. Characterizing genetic diversity

The effects of farming practices on manioc genetic diversity were evaluated using general statistics developed for population genetics[17]. *F*-statistics (Weir & Cockerham 1984), observed ($H_O$) and expected ($H_E$) heterozygosities (Nei 1978), allelic frequencies and allelic richness ($A_R$) were computed using FSTAT 2.9.3 (Goudet 1995). Population differentiation tests were performed for all landraces for which $N \geq 10$ in FSTAT by permuting genotypes amongst populations 5,000 times. Significance of *P*-values was adjusted using Benjamini and Hochberg's sharpened test (2000).

Allelic richness $A_R$ was computed using the rarefaction index proposed by El Mousadik and Petit (1996). For comparison between villages, allelic richness ($\hat{A}$) was estimated after clonal replicates were removed from the samples (treating each village independently) and the sample size standardized to a common threshold, using the multiple random reduction method proposed by Leberg (2002).

Genotypic diversity was evaluated using the clonal richness index, *R* (Dorken & Eckert 2001), calculated as follows:

$$R = \frac{(G-1)}{(N-1)} \qquad [5]$$

where *G* is the number of distinct MLGs, and *N* the number of samples. Independently of sample size, *R* will always be 0 for a strictly monoclonal landrace.

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[17] Estimation of parameters is dependent upon the evolutionary model assumed for microsatellites mutation. The infinite allele model (IAM) holds that each mutation creates any new allele, contrary to the stepwise-mutation model (SMM), in which mutation adds or substrates a single unit from the allele. Generally, the SMM is assumed where size matters, i.e., where two alleles similar in size are more closely related that two alleles very different in size.

Different models fit different loci. Composite repeats seem to follow the IAM, while the SMM is more fitted to 2-5 bp repeats. Most markers used in this study contain dinucleotide GA repeats (except SSR68 and SSR169; see table Appendix C1), very common in plants (Jarne & Lagoda 1996), and for which the alternative two-phase model (TPM) proposed by Di Rienzo *et al.* (1994) was shown to be a better approximation. However, given the short evolutionary scale of the phenomena studied in this thesis and the short number of generations considered, mutation is unlikely to play a major evolutionary role[*], and assuming either models (SMM or IAM) will not affect significantly the conclusions, and *F*-statistics, based on the IAM, were used throughout the thesis. Similarly, homoplasy* has little effect on populations over a short period of time (hundreds of generations).

[*] See also the final discussion in Chapter VI.

### 2.2.6. Assessing the role of manioc volunteers

Manioc volunteer seedlings usually appear within the two weeks that follow burning (Elias & McKey 2000, Pujol *et al.* 2002), then density of volunteers rapidly decreases as the field gets older (Pujol *et al.* 2005, 2007). In order to assess the impact of the farming system on ecological opportunities for the incorporation of seedlings into the stock of planting material, I estimated the density of manioc volunteers in the farms.

*Density of manioc volunteers in the farms*

I conducted careful searches for volunteer seedlings in every new field (opened within the last six months). In each field, I randomly selected five $4m^2$ quadrats, and counted all seedlings within the quadrats. Wherever seedling densities were too low and/or seedlings too scattered over the field, I undertook exhaustive counting of volunteers over the whole parcel. I then calculated densities with regard to the size of the field.

*Genetic diversity of manioc volunteers*

While estimating density in the farms, I also sampled populations of volunteer seedlings from the quadrats, in order to analyze their genetic structure and assess their potential impact on the genetic diversity of manioc populations. Only cohorts of at least 30 plants were considered for genetic analyses. GENEPOP 3.4 (Raymond & Rousset 1995) was used to test departure of genotypic proportions from Hardy-Weinberg assumptions, and to test the significance level of $F_{IS}$ values by performing Fisher exact tests. Rate of selfing [18] was assessed for each population with the maximum likelihood method implemented in RMES (David *et al.* 2007). RMES derives an estimate of the selfing rate, *s*, from the multilocus structure of the sample, independent of $F_{IS}$, and thus free of technical artefacts (*e.g.*, null alleles* or allelic dropout*).

*Parent-offspring analysis*

Setting as potential 'mothers' the typical MLG of each landrace, I used CERVUS 3.0 (Kalinowski *et al.* 2007) to run parentage analyses (maternity analysis with unknown father) and identify the most likely 'mother', that is, the landrace that produced the seeds. CERVUS uses a likelihood-based approach to assign parentage, and therefore allows for typing errors.

[18] In traditional manioc farms, planting of manioc landraces in monovarietal patches favours geitonogamy, *i.e.*, cross-pollination among clonemates, which accounts for apparent selfing (Pujol *et al.* 2005b).

The program runs simulation (100,000 iterations) of parentage analysis to determine the confidence of parentage assignments, and calculates log of odds (LOD) scores by taking the natural log of the overall likelihood ratio, that is, the likelihood that the candidate parent is the true parent divided by the likelihood that the candidate parent is not the true parent. A LOD score of zero means that the candidate parent is equally likely to be the true parent as any randomly selected potential parent. A positive LOD means the candidate parent is more likely to be the true parent than not the true parent. The statistic used for inferring parentage is the difference (delta) between LOD scores of the most likely parents. Delta is tested against critical values derived by simulation.

When running parentage analyses, I assumed that 1) ownership of the parcel where volunteers were collected had not changed over the past two years, and 2) that the farmer did not change in a significant way the set of manioc landraces he plants in his fields over the last two years. Information about the previous cultivation history of the fields where seedlings were sampled was collected during interviews.

# 3. The bewildering diversity of manioc in Gabon

In Gabon, like in other parts of Africa (see Chiwona-Karltun *et al.* 1998, Mkumbira *et al.* 2003) and in many Amerindian tribes (Boster 1984a,b, 1986, Heckler 2004), manioc is a woman's crop (Salick *et al.* 1997, Heckler & Zent 2008). Although every member of the family may help with specific tasks at various stages of the agricultural calendar, most agricultural tasks (and processing) are performed by women, who hold the folk taxonomical knowledge on manioc landraces[19].

I interviewed in total 191 farmers, most of whom were women (see Appendix B1), and recorded 355 distinct names of manioc landraces, including 212 landraces that farmers categorized as "bitter". Binot (1998) listed eight further names in La Lopé; Van der Veen and Bodinga-bwa-Bodinga (2002) recorded near Fougamou two names that I did not record in the nearby villages of Douani and Mandilou; and Soengas (2010) mentioned 23 additional names in Ekata. Taking into account that some of these names may be synonymous with landrace names I have recorded, this gives a total of 406 names (228 bitter landraces). A complete listing of landrace names recorded in Gabon is presented in Appendix B4.

Seventy-six landrace names were locally considered as synonyms of one or more other landrace names (*e.g.*, '*Matati*', '*Akwama-Mbõng*' and '*Afouba-Mbõng*' in Mbong-Ete, '*Kaioio*' and '*Okukuia*' in Odjouma), and 105 landraces bore names similar to that of at least one other landrace, often reflecting a change in the pronunciation between different dialects (*e.g.*, '*Djogo*' [Teke, B.71], '*Nzoghu*' [Myènè, B.11], '*Zôk*' or '*Zoku*' [Kwele, A.85b]). I also recorded 18 cases where several morphologically distinct landraces were being given the same name (*i.e.*, morphotypes), but farmers distinguished between them by adjoining an epithet to underline the main phenotypic difference between two such 'morphotypes' (*i.e.*, '*Mutõmbi* black' and '*Mutõmbi* white').

Sometimes farmers could not recall the name of a landrace, and I counted in total 45 "unknown" manioc landraces, 25 of which I recorded in a single village (Mopia). Farmers also mentioned five landraces allegedly "lost" ('*Ayima*', '*Boko A Poto*', '*Anãnga*', '*Mugwendje*', '*Pokwe*').

[19] The selection of planting material and the management of landraces in the field being generally the monopoly of women, by farmer I will henceforth designate women, unless stated otherwise.

## 3.1. The amplitude of manioc diversity in Gabon

Several of the nearly 400 manioc appellations I listed were probable variants or alternative names (*i.e.*, synonymies) of the same clone (or set of clones). Besides, most of this tremendous diversity was local, and only about 10% (42) of the names I recorded were actually shared by two or more villages. I also found no landrace that was shared by all the communities I surveyed. Remarkably, all the most widespread landraces ('*Okwata*', '*Matadi*', '*Dame Jaune*') were categorized as sweet, and I did not find any similar case of a bitter landrace being shared by more than two communities.

### 3.1.1. Variations across communities

The number of landraces per village was high, but also quite variable among villages (37 landraces on average, with a variation of ± 15 landraces across communities; Table 2.1). The number of landraces varied between eight (Mbong-Ete) and 60 (Odjouma). Except in the case of Mbong-Ete, rarefaction curves never reached a plateau (Figure 2.2), suggesting that the figures I report for each village underestimate the actual diversity of manioc landraces at the local level.

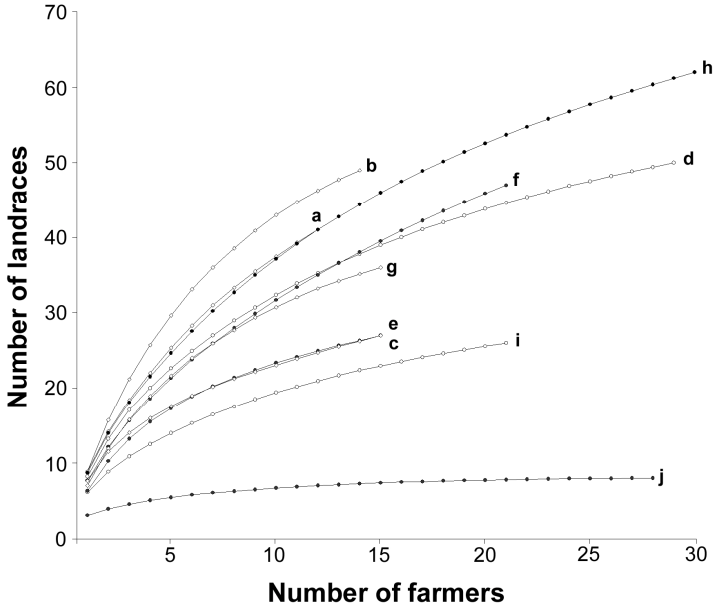


**Figure 2.2. Saturation curves** for the ten villages studied (a. Odimba, b. Nombedouma, c. Douani, d. Mandilou, e. Makoula, f. Mopia, g. Mouyabi, h. Odjouma, i. Imbong, j. Mbong-Ete).

Bitter varieties accounted for half the diversity of manioc in the farms (53%). However, I noticed here also strong variations across communities. Bitter manioc represented 83% of the landraces grown by Teke [B.71] farmers in Odjouma, but only 19% of the manioc landraces grown by Tsogho [B.31] farmers in Douani (Figure 2.3).

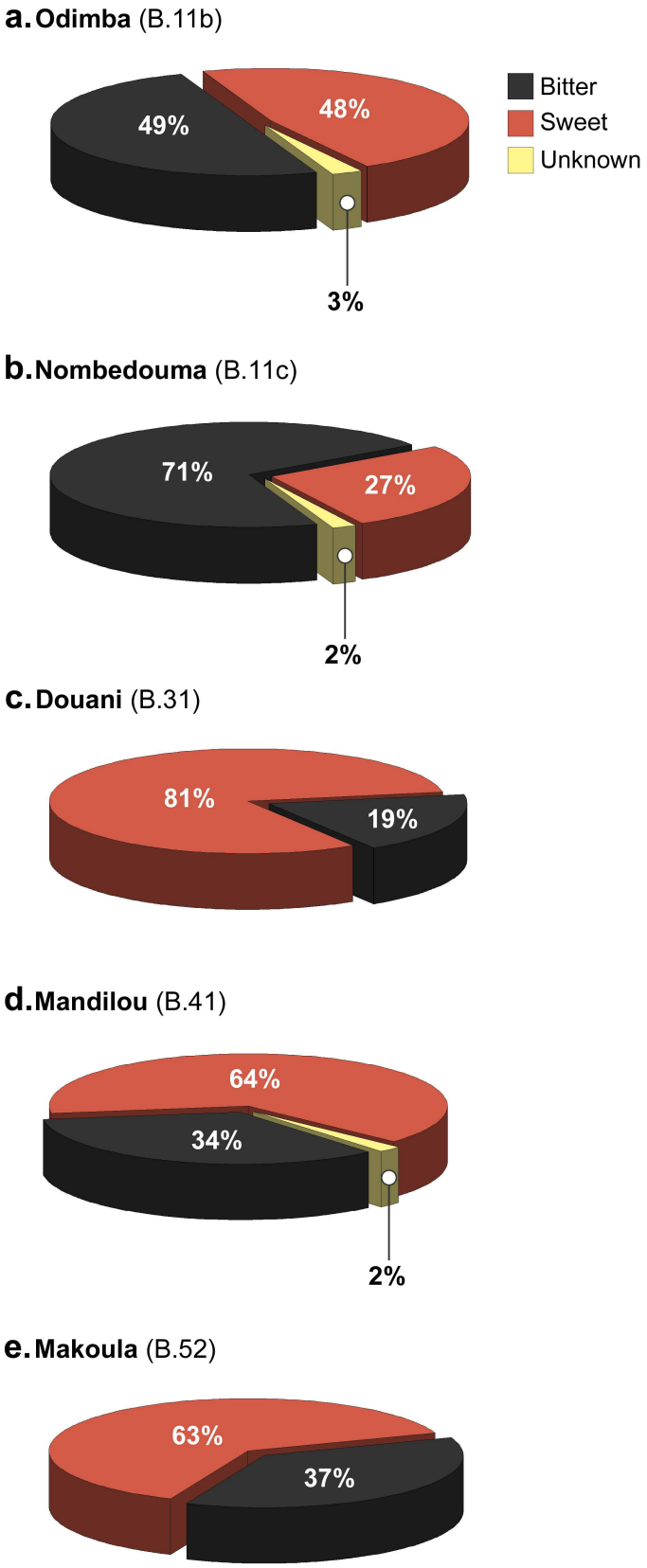


**Figure 2.3. Variation across villages of the ratio between bitter and sweet manioc landraces**. Note that caution is required as the bitter-sweet ratio is not telling of the relative importance of each category in the farms (*i.e.*, difference in planting density).

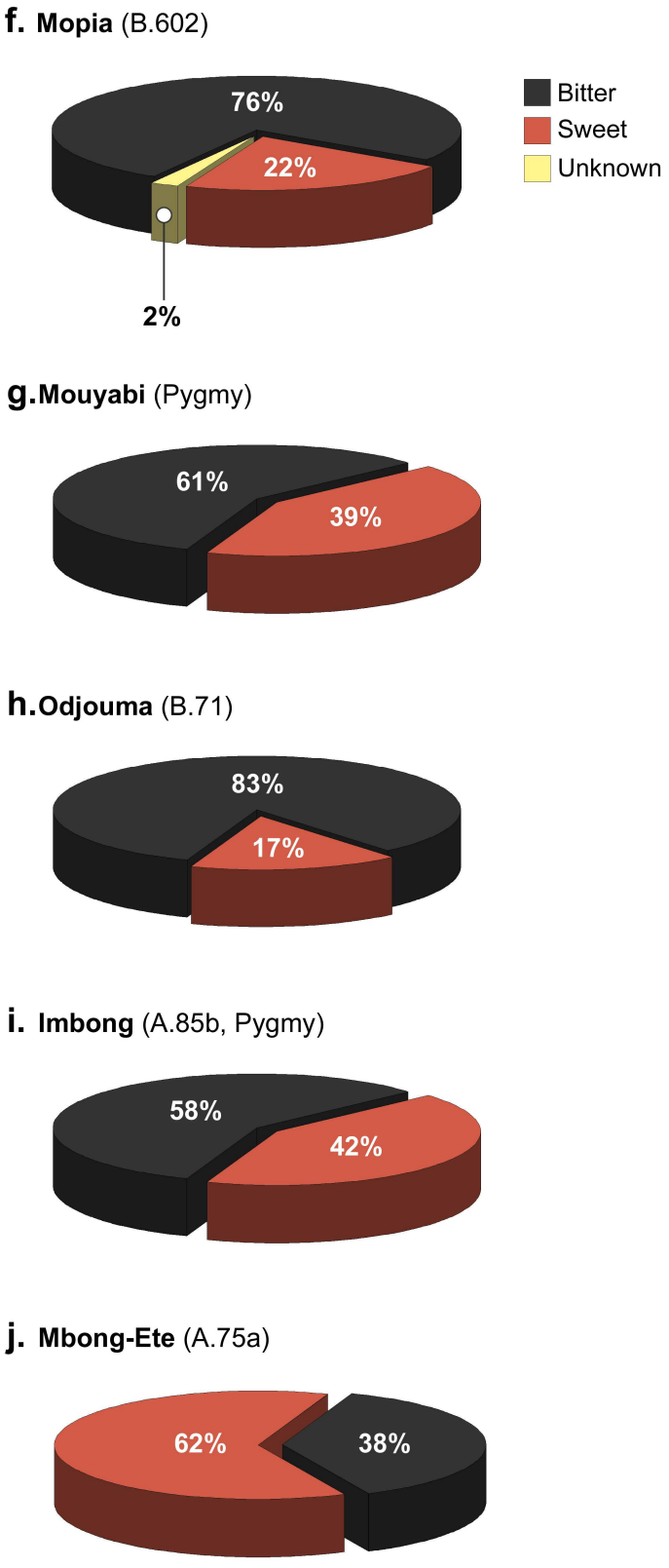


**Figure 2.3** (continued)**. Variation across villages of the ratio between bitter and sweet manioc landraces**. Note that caution is required as the bitter-sweet ratio is not telling of the relative importance of each category in the farms (*i.e.*, difference in planting density). In Mbong-Ete (j), bitter manioc predominates, with two landraces accounting together for more than 80% of the total area planted with manioc.

### 3.1.2. Variations among farmers

Values of the evenness indexes ($E_v$ and $E_f$) echoed also strong disparities between farmers' collections[20] of landraces at the community level, but not as much in terms of number of landraces grown by each farmer ($7 \pm 4$), which tended to be overall relatively homogeneous (average $E_f = 0.91 \pm 0.05$), as in the distribution of varietal diversity among farmers (average $E_f = 0.63 \pm 0.10$). Farmers shared only a small fraction of the total diversity present at the village level, and 145 (39%) of the landraces I recorded were grown by only one farmer. At the community level, such 'private' landraces accounted on average for 35% of the total diversity present in the village (ranging from 0% in Mbong-Ete, where all farmers grew the same landraces, to 53% in Odimba).

## 3.2. Evolution of manioc diversity since 1960

Diachronic data are difficult to collect. However, some information on manioc landraces grown in Gabon in the past can be found in Raponda-Walker and Sillans (1961) and Sautter (1966)[21]. Although their lists are unlikely to be exhaustive, and probably also overlook synonymies, they provide valuable information on the evolution of manioc diversity since 1960.

Many of the names Raponda-Walker and Sillans recorded in 1961 are still found nowadays. The landrace '*Putu*', in particular, which I found in two Myènè communities, Odimba [B.11b] and Nombedouma [B.11c], is also listed among the Mpongwe [B.11a] and the Nkomi [B.11e]. Gaulme (1981) also mentions '*Putu*' as a popular landrace in the Fernan-Vaz twenty years later. Among the Tsogho [B.31], Raponda-Walker and Sillans cited '*Epãndo*' and '*Oabe*' in 1961, both of which Van der Veen and Bodinga-bwa-Bodinga (2002) mentioned, forty years later, among the Eviya [B.301], and both of which I also found in Douani among the Tsogho [B.31]. Compared to the 37 landraces I recorded, on average, in the ten villages I surveyed forty years later, the seven landraces reported by Raponda-Walker and Sillans (1961) suggests a considerable enrichment of manioc varietal diversity since the 1960s.

[20] That is, the set of varieties a farmer manages in his farms.

[21] I included these lists, as well as those of Angladette (1949), Guillot (1970), Adam (1980), Gaulme (1981), Dounias (1993), Binot (1998), Van der Veen & Bodinga-bwa-Bodinga (2002), Soengas (2010), in Appendix B4.

**Table 2.1. Amplitude of manioc diversity** in the 10 study sites. Only the ten most popular (*P*, frequency among farmers) landraces are indicated*.

| **Province** | Ogooué-Maritime | Ogooué-Maritime | Ngounié |
|---|---|---|---|
| **Village** | Odimba | Nombedouma | Douani |
| **Ethnic group** | | | |
| Majority | Myènè Orungu [B.11a] | Myènè Galwa [B.11b] | Tsogho [B.31] |
| Minorities | Vili [H.12] | | Eviya [B.301] |
| | Akele [B.22] | | Ghisir [B.41] |
| | Nkomi [B.11e] | | |
| **Estimated population** (density) | 100 (6-8 inhabitants x $km^{-2}$) | 300 (1-2 inhabitants x $km^{-2}$) | 150 (2-4 inhabitants x $km^{-2}$) |
| **Agro-ecological environment** | Mangroves | Forest | Forest |
| **Main source of income** | Farming | Logging (private) > fishing > farming | Logging (wage-labour) |
| **Number of landraces** | 40 (at least 6 unknowns) | 48 (3 unknowns) | 32 |
| Ratio bitter/sweet | 20/19 (1 undetermined) | 34/13 (1 undetermined) | 6/26 |
| Average | 9 | 9 | 8 |
| Minimum | 2 | 2 | 4 |
| Maximum | 20 | 19 | 11 |
| **Index of evenness** | | | |
| $E_v$ | 0.65 | 0.79 | 0.69 |
| $E_f$ | 0.87 | 0.88 | 0.96 |
| **Landraces grown by one farmer** | 21 | 18 | 12 |
| **Landraces grown by all farmers** | 2 | 0 | 0 |
| **Popular landraces** (*P*) | *Matadi* (100) | *Okwata* (71) | *Mutõmbi* (93) |
| | *Lãndi-Lãndi* (100) | *Ntse-Putu* (57) | *Dikilikoko Di Chinois* (80) |
| | *Bakõngo* (67) | *Otãngani* (50) | *Etadi* (73) |
| | *Madouedoue* (67) | *Atolizo-Ozõmbi* (43) | *Mounzoumba* (73) |
| | *Timba Jaune* (67) | *Premier Choix* (36) | *Mana* (67) |
| | *Owãntope* (67) | *Bakõngo* (36) | *Kwata* (60) |
| | *Ndzao Re Bimbia* (42) | *Matadi* (29) | *Maboundinieghe* (47) |
| | *Ntselele* (25) | *Ogulungu* (29) | *Dikilikoko Di Jaune* (33) |
| | *Okwata* (25) | *Nzoghou* (29) | *Oabe* (27) |
| | *Kumba Mavungu* (25) | *Ighozo* (21) | *Simbu* (27) |

See Appendix B4 for a complete listing of landraces recorded in each study site.

**Table 2.1.** (continued)

| **Province** | Ngounié | Ogooué-Lolo | Haut-Ogooué |
|---|---|---|---|
| **Village** | Mandilou | Makoula | Mopia |
| **Ethnic group** | | | |
| Majority | Ghisir [B.41] | Ndzabi [B.52] | Tsaayi [B.73a], Kaningi [B.602] |
| Minorities | Punu [B.42] | Bongo (Pygmy) | Wumbu [B.77], Kota [B.25], Mbamba [B.62] Ndasa [B.28], Mbanwe [B.23] |
| **Estimated population** (density) | 400 (4-6 inhabitantsxkm$^{-2}$) | 200 (1-2 inhabitantsxkm$^{-2}$) | 400 (6-8 inhabitantsxkm$^{-2}$) |
| **Agro-ecological environment** | Forest | Forest | Forest |
| **Main source of income** | Logging (wage-labour) | Logging (wage-labour) | Logging (wage-labour) > subsistence |
| **Number of landraces** | 50 (1 unknown) | 27 | 46 (26 unknowns) |
| Ratio bitter/sweet | 17/32 (1 undetermined) | 10/17 | 35/10 (1 undetermined) |
| Average | 8 | 6 | 8 |
| Minimum | 2 | 3 | 4 |
| Maximum | 17 | 16 | 11 |
| **Index of evenness** | | | |
| $E_v$ | 0.58 | 0.70 | 0.57 |
| $E_f$ | 0.88 | 0.87 | 0.97 |
| **Landraces grown by one farmer** | 16 | 10 | 23 |
| **Landraces grown by all farmers** | 0 | 1 | 1 |
| **Popular landraces** (*P*) | | *Yala* (100) | *Pauline* (100) |
| | *Ditadi* (79) | *Benge* (60) | *Jaune* (76) |
| | *Kwata Igulu* (69) | *Litedi* (53) | *Lekaga* (71) |
| | *Kwata Mayumba* (66) | *Gobatchikà* (47) | *Mussala* (52) |
| | *Simbu* (59) | *Muvovodi* (40) | *Leboyo* (43) |
| | *Ndungu* (52) | *Dame Jaune* (33) | *Mwagãnga* (38) |
| | *Bata* (48) | *Dinjãnga* (33) | *Moungebe* (38) |
| | *Mutõmbi* (48) | *Wakwãngu* (27) | *Mupele* (29) |
| | *Brazzaville* (34) | *Brazzaville* (27) | *Mountzãnga* (14) |

**Table 2.1.** (continued)

| **Province** | Haut-Ogooué | Haut-Ogooué | Ogooué-Ivindo | Woleu-Ntem |
|---|---|---|---|---|
| **Village** | Mouyabi | Odjouma | Imbong | Mbong-Ete |
| **Ethnic group** | | | | |
| Majority | Bongo (Pygmy) | Teke [B.71] | Kwele [A.85b] | Fang Ntumu [A.75a] |
| Minorities | | | Mwessa [B.20] | |
| | | | Koya (Pygmy) | |
| **Estimated population** (density) | 250 (2-4 inhabitants x $km^{-2}$) | 150 (0-1 inhabitants x $km^{-2}$) | 200 (1-2 inhabitants x $km^{-2}$) | 400 (8-10 inhabitants x $km^{-2}$) |
| **Agro-ecological environment** | Savannah-forest transition | Savannah-forest | Forest-swamp | Forest |
| **Main source of income** | Subsistence | Subsistence | Farming > subsistence | Farming |
| **Number of landraces** | 36 (5 unknowns) | 60 (2 unknowns) | 26 (3 unknowns) | 8 |
| Ratio bitter/sweet | 22/14 | 50/10 | 15/11 | 3/5 |
| Average | 7 | 9 | 6 | 8 |
| Minimum | 5 | 3 | 3 | 2 |
| Maximum | 10 | 32 | 12 | 5 |
| **Index of evenness** | | | | |
| $E_v$ | 0.74 | 0.53 | 0.55 | 0.50 |
| $E_f$ | 0.96 | 0.83 | 0.92 | 0.97 |
| **Landraces grown by one farmer** | 13 | 23 | 9 | 0 |
| **Landraces grown by all farmers** | 0 | 0 | 1 | 1 |
| **Popular landraces** (*P*) | *Pauline* (73) | *Õngania* (81) | *Mañebwe* (100) | *Esobo-Nku* (100) |
| | *Kãmi* (67) | *Kaioio* (77) | *Bana* (91) | *Adzoro* (96) |
| | *Mwagãnga* (47) | *Oyagija* (74) | *Mbwasia* (86) | *Akwama-Mbõng* (39) |
| | *Leboyo* (47) | *Lãngori* (68) | *Gõndoyem* (57) | *Afouba-Mbõng* (32) |
| | *Konõngo* (40) | *Opipi* (61) | *Dinbata* (57) | *Matati* (18) |
| | *Mokoyo* (33) | *Ochemi* (58) | *Akumikara* (29) | *Dame Alice* (7) |
| | *Lekaga* (27) | *Ossoele* (39) | *Ãndamebeka* (24) | *Dame Jaune* (7) |
| | *Dame Jaune* (27) | *Djalabumi* (23) | *Kãngole* (19) | *Nkot-Mbõng* (7) |
| | *Likaga* (20) | *Bõngo* (16) | *Akunuku* (19) | — |
| | *Lekõndo* (20) | *Oielekunda* (16) | *Afún* (14) | — |

## 3.3. Sourcing diversity

Farmers can source 'seed' (here in the sense of propagules) through different networks, most of which involve exchanging germplasm with other farmers, but may also recruit new clones among manioc volunteers that appear spontaneously in their manioc farms.

### 3.3.1. Farmers' informal 'seed' systems

I investigated the origins of the landraces my informants grew. In most villages in Gabon, farmers held a 'core' collection of landraces, bequeathed from their parents. Although transmission was predominantly vertical (mothers to daughters, Figure 2.4), farmers continually 'personalized' their collection of landraces, and enriched it by soliciting cuttings from relatives or neighbours, or by seeking outside the village new landraces to try (*e.g.*, the Tsogho [B.31] in Douani, the Galwa [B.11c] in Nombedouma, and the Teke [B.71] in Odjouma). Such horizontal transfers of cuttings represented about one-third of all exchanges of landraces at the community level. Even though farmers often obtained cuttings from several sources, 70% of the 191 farmers I interviewed had obtained all or most of their cuttings from a single source, in majority (60%) from their mother. In Mbong-Ete (Fang Ntumu [A.75a]), affinal transmission (*i.e.*, the transfer of landraces from mothers-in-law to daughters-in-law) was however predominant (see Chapter V).

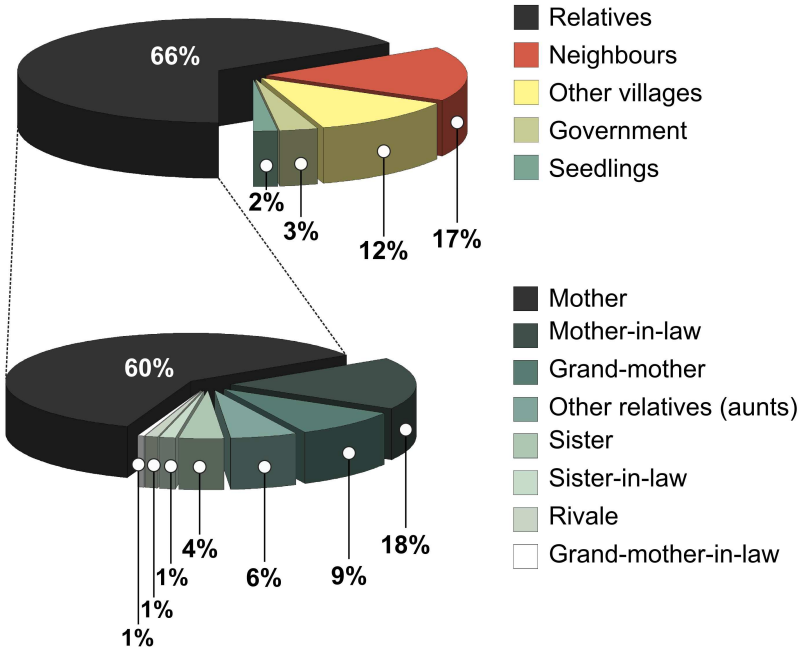


**Figure 2.4. Origin of manioc cuttings for 191 farmers** (percentage of the total number of exchanges, $N = 254$). Details are given for the "relatives" category in the lower pie chart. "Rivale" designates concubine in polygynous households.

### 3.3.2. Variations in perception of manioc volunteers

Manioc volunteer seedlings represented a very minor source of new landraces for farmers in Gabon (only 2%). But while most farmers discarded manioc volunteer seedlings from their farms (54% of the 191 farmers interviewed), their behaviours towards manioc volunteers varied considerably among communities (Figure 2.5).

In Odimba (Myènè Orungu [B.11b]) and in Nombedouma (Myènè Galwa [B.11c]), farmers fostered the growth of manioc seedlings in their farms (Figure 2.5a,b). In contrast, farmers in Douani (Tsogho [B.31]) and in Mbong-Ete (Ntumu [A.75a]) systematically weeded manioc volunteers (Figure 2.5c,j). In Odjouma (Teke [B.71]), a large proportion of farmers (43%) ignored the existence of manioc volunteers, and failed to notice them in their farms (Figure 2.5h). Odjouma was actually the sole village in Gabon where some farmers had never noticed, or paid attention to, manioc volunteers[22]. In all other villages, farmers knew about manioc flowers, fruits and seeds, but more than 40% (66/155) nevertheless believed volunteers to be resurgences of old cuttings, and believed manioc seeds to be sterile.

With the Myènè (Odimba and Nombedouma) being an exception to the rule, manioc volunteer seedlings in Gabon were rarely actively selected for. Instead, the majority of farmers (54% of the 191 farmers interviewed) weeded volunteers in their farms. Behaviours towards volunteers varied greatly among farmers, even within villages, and generally reflected idiosyncratic beliefs or knowledge about manioc volunteers.

Farmers' behaviours could be schematized as a dichotomous decision tree[23] (Figure 2.6). Whether farmers engaged along one or another of these different chains of behaviours depended mostly on farmers' intimate knowledge about manioc volunteers. Hence, farmers who believed volunteers to be a resurgence of cuttings were more prone to foster volunteers in their farms (21/66) than farmers who knew manioc volunteers to be true seedlings (17/89).

[22] Data from Odjouma are taken from a previous work and were included for comparison. Further information and discussion can be found in Delêtre (2004).

[23] Values reported on the tree are those pooled for my entire sample (191 farmers).

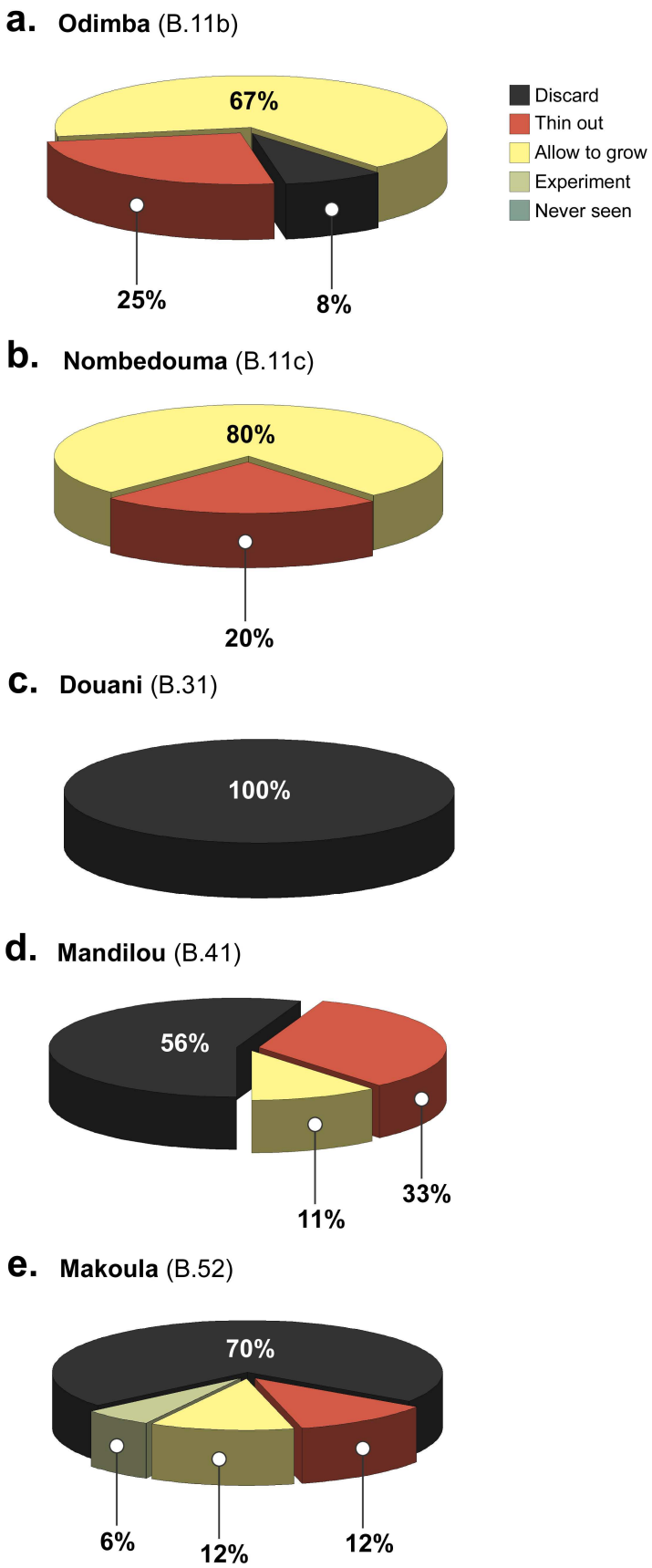


**Figure 2.5. Comparison of farmers' behaviours towards manioc volunteers**. For Odimba $N = 12$, for Nombedouma $N = 14$, for Douani $N = 15$, for Mandilou $N = 18$, for Makoula $N = 16$. The dominant ethnic group is indicated between brackets.

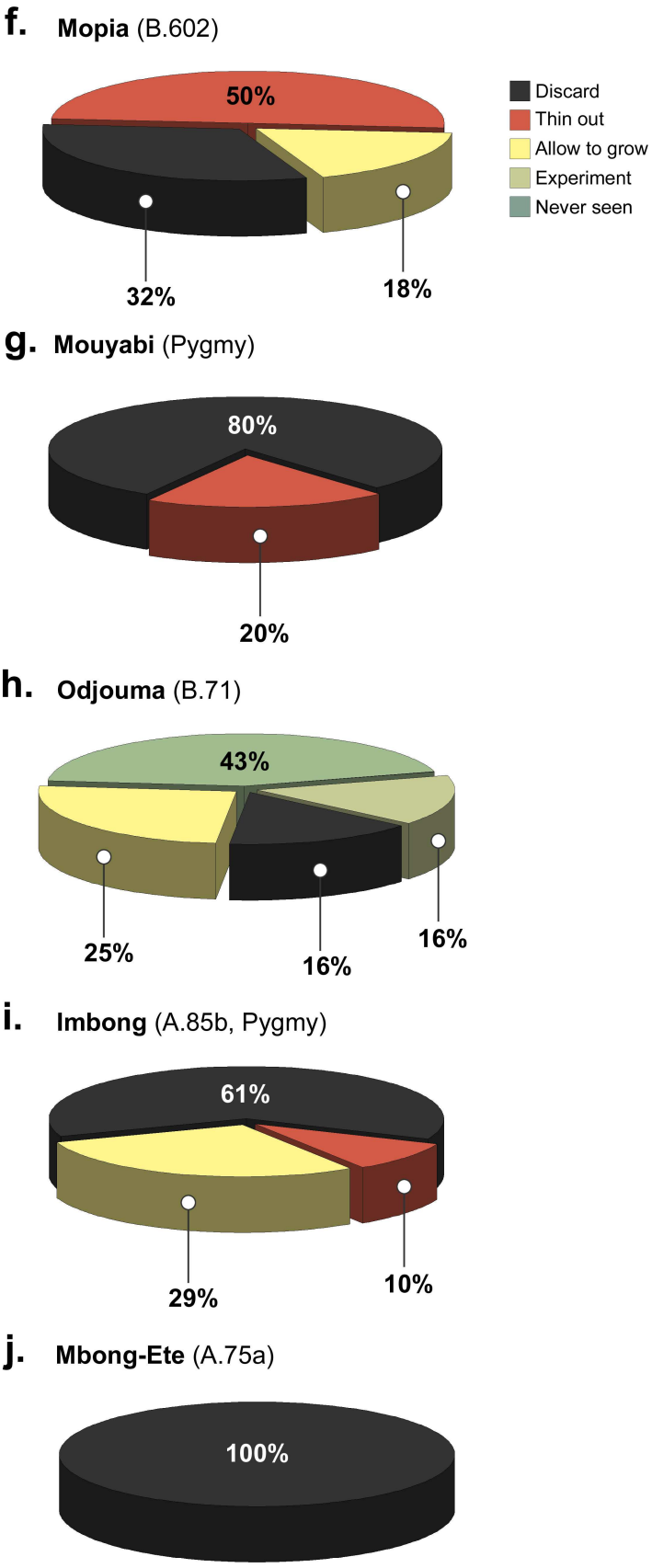


**Figure 2.5** (continued)**. Comparison of farmers' behaviours towards manioc volunteers** (continued) (Mopia: $N = 21$, Mouyabi: $N = 15$, Odjouma: $N = 31$, Imbong: $N = 21$, Mbong-Ete: $N = 28$) The dominant ethnic group is indicated between brackets.

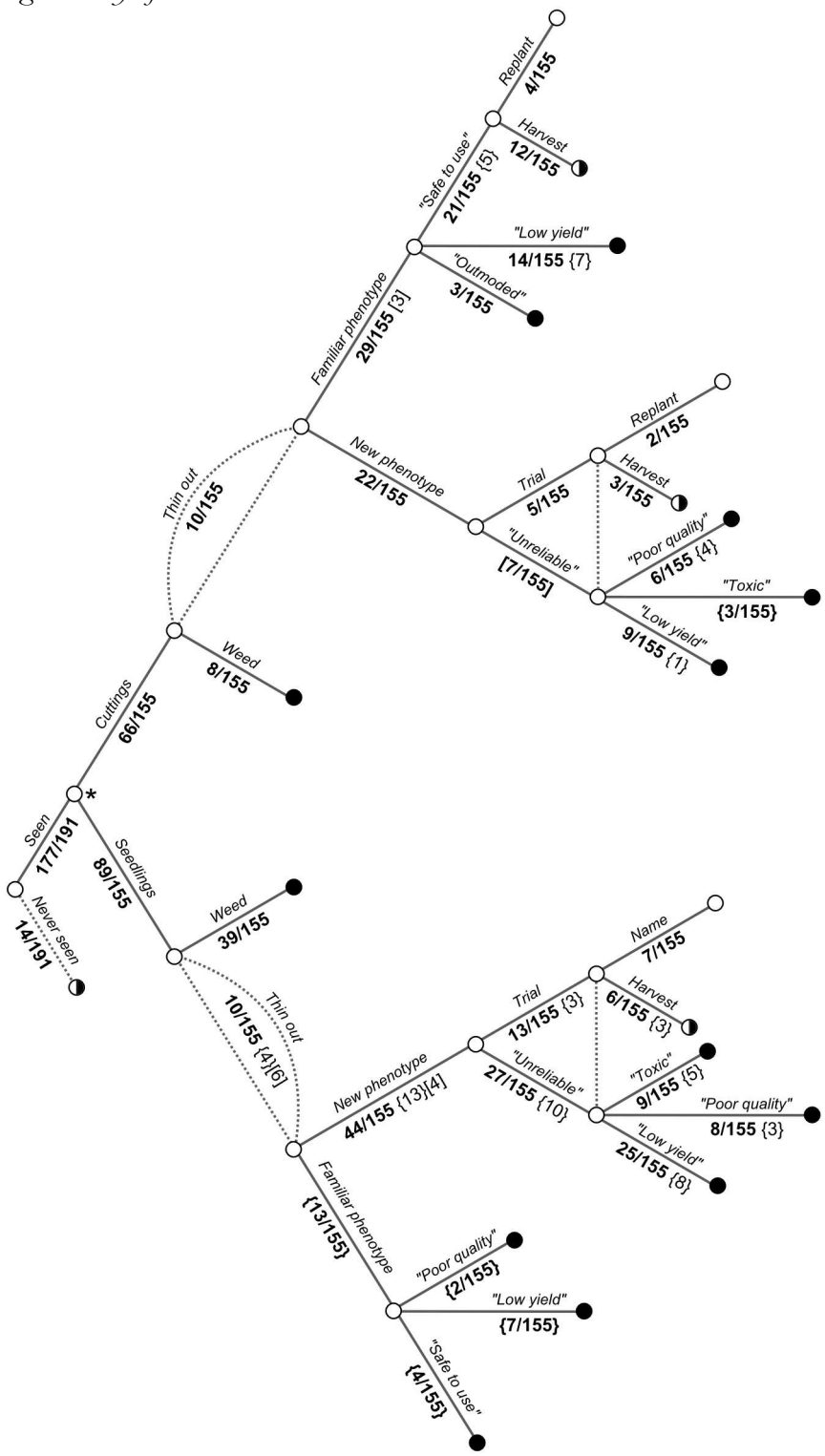


**Figure 2.6. A dichotomous representation of farmers' behaviours towards manioc volunteers**. The proportion of farmers interviewed that engaged in a particular behaviour is indicated. ***** Data is available only for 155 of the 191 farmers interviewed. [x] indicates that x farmers did not give any further explanation. {x} indicates that x farmers engaged in several different behaviours. ● indicates where volunteers are discarded. ○ indicates where volunteers are left to grow, and may be multiplied after harvest. ◑ indicates where volunteers may be replanted after harvest. Note that an implicit distinction is made between volunteers that are multiplied and volunteers that are replanted. The former suggests that farmers recognize the novelty of volunteers' morphological features and will manage them as independent entities (possibly by giving them a name) while the latter implies that the volunteers are simply assimilated to known landraces and used as a source of planting material.

# 4. The paradox of diversity in African manioc farms

"Hyperdiversity" (Brush 1992) is a common feature of manioc farming systems in Amazonia, where several authors have documented considerable diversity of manioc landraces in Amerindian farms (Boster 1984b, Chernela 1986, Kerr 1986, Salick *et al.* 1997, Emperaire *et al.* 1998, Elias *et al.* 2000a). It is, however, uncommon in Africa.

Between 1989 and 1991, a collaborative study of manioc (COSCA) surveyed local manioc farming systems in ten African countries that altogether account for more than two-thirds of total manioc production in Africa[24], and recorded about 2,800 named landraces, with values ranging from 175 landraces for Ghana to 423 for Malawi (Nweke 1994). However, when considering the number of villages surveyed in each country, mean values of varietal diversity per village ranged between four (Ghana) and eight (Tanzania), that is, values much below those I report for Gabon.

For Africa, the diversity of manioc in Gabon is thus among the highest ever reported at the village level. Diversity averaged 37 landraces, but in one single village (Odjouma), I recorded up to 60 different names, that is, levels of named diversity comparable to that found in Amerindian manioc farms (see Boster 1984b, Chernela 1986, Emperaire *et al.* 1998, Elias *et al.* 2001a). With the particular exception of Mbong-Ete (northern Gabon), where I found the lowest varietal diversity (eight landraces at the community level, and only three landraces per farmer), farmers in Gabon maintained on average seven landraces (ranging between six in Imbong and nine in Odimba), some growing up to 30 different landraces in their farms (in Odjouma). In Ghana, Manu-Aduening *et al.* (2005) found at most nine landraces per village and, on average, only four landraces per village, and only one or two landraces per farmer.

High levels of named diversity, however, do not necessarily imply high levels of genetic diversity. There are several mechanisms through which diversity can be increased regionally and locally, the most important of which is the dissemination of landraces alongside with the flow of people.

[24] The survey covered Burundi, DR Congo, Côte d'Ivoire, Ghana, Kenya, Malawi, Nigeria, Tanzania, Uganda, and Zambia.

Exchanges of cuttings between farmers were extremely frequent in Gabon, and represented the principal medium for farmers to acquire new landraces. But repeated and independent introductions of the same landrace in a village, or the simple deformation of the original name while the landrace passes down the generations and circulates among farmers, can generate synonymies, thereby artificially increasing diversity.

## 4.1. Names along the grapevine

Names of landraces are contextual. They evolve along a landrace's journey through time and space (Boster 1984b, Salick *et al.* 1997, Manusset 2006). Names of landraces are versatile, precisely because cuttings are continuously exchanged between farmers, between villages and between communities, sometimes over long distances [see for example the Teke in Gabon (Delêtre 2004, Delêtre & McKey submitted), but also Chernela (1987) and Emperaire & Peroni (2007) in Brazil]. The name is altered as it is adapted to different dialects. '*Dikilikoko*', '*Eake A Tchosso*' and '*Make Ta Koko*', for example, are three translations (in Ghisir [B.41], in Tsogho [B.31] and in Punu [B.43], respectively) of the same name, "egg yolk". A name may also completely change, so as to reflect how the cutting was brought to the village, or as a way to acknowledge the farmer who introduced it (Boster 1984b, Elias *et al.* 2000). Likewise, in Odimba, the landrace '*Bõndjolãmba*' is sometimes called '*Assidieke*', from the name of the woman who brought the cuttings from the village of Bondjolamba[25].

Renaming landraces is a very common practice (Kizito *et al.* 2007a), and the same landrace can be found under a large variety of appellations. '*Ngungu Remba*' (recorded by Sautter in 1966 in Nombedouma and by myself in 2007 in Odimba, Douani and Mandilou), is also called '*Oguka*', '*Digõndi*', '*Rizõmbo*' (after the person who introduced it), '*Karonari*' (after the village where Rizombo found the cutting), '*Mõngiloti*' (from the Myènè **mõngo'iloti**, literally "potato manioc"), '*Ndjawebimbia*' or '*Ndzao Re Bimbia*', as the pronunciation changes between Punu [B.43] and Ghisir [B.41].

Exchanges thus contribute to enrich named diversity. When a landrace changes name, the original meaning may remain, but the connection between the two names may be forgotten with time, thereby creating synonymies which lead to overestimating the number of landraces, and complicates the task of evaluating the actual diversity at the

[25] Another example is '*Maya*' (the name of the farmer who 'discovered' the landrace), which some farmers also call '*Luanda*' (the village from where Maya brought the landrace).

country scale. Names can even change between households within the same community (Boster 1984b, Salick *et al.* 1997). Folk taxonomies, therefore, rarely reflect the underlying genetic diversity, and it is wise not to directly apply a biological dimension to the local folk taxonomies of crop landraces, and to always differentiate "cultural landraces"[26] from "natural landraces"[27] (*sensu* Manusset 2006), which is the purpose of the combined approach I followed to investigate how much the wealth of names for manioc landraces reflected the true genetic diversity of manioc in Gabon.

## 4.2. Sourcing diversity: the African conundrum

One the most surprising outcomes of the general survey I undertook in Gabon was the great variations I found across communities in the number of landraces they maintained in their farms, with levels of diversity ranging from values as extreme as eight, for Mbong-Ete, to 60 in Odjouma.

Several 'logics' may back up farmers' choices to maintain either high or low numbers of landraces in their farms, including agroecological constraints (Delêtre 2004), economic incentives (Salick *et al.* 1997, Emperaire *et al.* 1998, McKey *et al.* 2001, Manusset 2006), or social factors (Heckler & Zent 2008). Ecological and socioeconomic factors are, however, only limited explanatory variables, and cannot alone explain the strong quantitative but also qualitative variations in patterns of diversity that I found across villages in Gabon.

In previous studies of manioc diversity in Africa (*e.g.*, Manu-Aduening *et al.* 2005), the authors have not attempted to identify the rationales behind farmers attitude to manioc diversity, or the origin of the levels of diversity they documented. Nor did they explain why African farmers rarely see manioc volunteer seedlings as a potential source of diversity (outside anecdotal personal initiatives, as in de Waal *et al.* 1997).

It is rather paradoxical that while most African manioc farmers seem to value diversity, and strive to collect and test new landraces (Kizito *et al.* 2005, 2007, Mkumbira *et al.* 2003, this study), they often lack interest in manioc volunteer seedlings (see Manu-Aduening *et al.* 2005), and rely instead on cuttings they source from other farmers, predominantly from within the community (Figure 2.4), but also from outside the village.

[26] Which differ by their names, not necessarily by their genotypes.

[27] Which, conversely, differ by their genotypes, but not necessarily by their names.

Behaviours towards manioc volunteers varied greatly among farmers I interviewed. In Ghana, Manu-Aduening *et al.* (2005) found similar strong variations in behaviours towards manioc volunteers among Ghanaian farmers. As I stressed in Chapter I, a detailed knowledge of manioc's ecology is not of immediate use to farmers, especially as clonal propagation generally provides a simple and straightforward means for renewing the stock of propagules. Hence, unless driven by necessity, such as scarcity of planting material (*e.g.*, Manu-Aduening *et al.* 2005) or the loss of the original varieties following a natural catastrophe, *e.g.*, fire, drought, epiphytotics (*e.g.*, Jennings 1963, 1970), farmers have little need for volunteers, and will only start experimenting with them if they develop a curiosity for them. Such process constructs from farmers' own experience and personal appreciation of diversity, possibly explaining why behaviours vary so much even at the scale of a small community. Curiously, the most marked differences I found were however those that I observed *among* communities.

## 4.3. Re-contextualizing diversity

Both culture and experience play an important role in the development of folk knowledge (Ross *et al.* 2002), but at the root of farmers' attitudes to crop diversity is however the particular relationship African farmers have knit with the plant. Because the introduction of manioc was deeply intertwined with the rather turbulent course of the contacts between Europe and Africa, the determinants of this 'plant-person relationship' (Salick 1995) are not just cultural, they are also largely contextual, and much depended on the particular socioeconomic and political circumstances surrounding manioc adoption by African societies.

Patterns of manioc diversity reflect culture-dependent differences in goals and values, which depend on the economic, social or cultural roles the plant has acquired in groups that have adopted it. They may also simply reflect the ventures of the history of the crop in the region of Africa, rather than the purposive actions of farmers on diversity. Understanding the dynamics of manioc diversity in Africa and evaluating the role of small-holders as the possible 'architects' of the crop's secondary diversification therefore requires being able to distinguish between the historical and cultural causes of the heterogeneous patterns of manioc diversity in Africa, and to investigate, beyond proximate causes, the true nature of cross-cultural variations in valuation of diversity. History, therefore, was probably an important factor in the emergence of Africa as a secondary centre of diversity for manioc, but this dimension has been so far overlooked.

## 4.4. Explaining the patterns: the historical approach

While analyzing my data, I realized that the patterns of manioc diversity in Gabon and, to a large extent also, variations among communities in their perception of manioc volunteers, could only be interpreted in the light of the historical trajectories of the crop's diffusion in Gabon, and by investigating the cultural and the socio-economic circumstances of the adoption of manioc by African populations. Hence, while the central question of this thesis—the dynamics of manioc genetic diversity—did not change, its transposition into the complex African context appeared to require approaching the problem within a historical perspective. The subject thus evolved from a question of evolutionary biology, seen in the light of ethnobotany, to something more relevant to the discipline of historical ecology, in which historical knowledge is used to explain the patterns of diversity we observe today.

Only few studies have contemplated the history of manioc in Africa (Jones 1959, Barampama 1992, Carter *et al.* 1992), and there is little information available from which the sequence of its adoption by African populations can be reconstructed. Yet, understanding variations among populations in the valuation of diversity requires reintroducing the comparative study of farming practices in the particular context of the diffusion of the crop among populations. An important part of my study has been therefore to document this history, and to gather and compile information on the trajectories of manioc's diffusion into and within Gabon. Drawing from this documentary research, I mustered several pieces of evidence that the modes of manioc spread among populations in Gabon were intricately linked with the progressive economic mutation of Gabon, as pre-colonial trade networks dissolved and Gabon evolved into a French colony during the 19$^{th}$ and 20$^{th}$ centuries.

### 4.4.1. Competing for work: manioc in colonial Africa

Several studies have shown that the basis of colonial economic expansion in Africa has been particularly conflicting with the traditional social organisation of African societies. By monopolizing the work-force for economic activities in the interest of the colony, the introduction of cash-crop agriculture, in several parts of Africa, was (and continues to be) particularly detrimental to local farming (Richards 1985). Tosh (1980) showed that the additional work-load from colonial agricultural policies, often carried out with strong, force-driven compulsion from the administration and little consideration for farmers'

customary obligations, was the main cause of the general abandonment of traditional cereals for less labour-intensive crops, such as manioc, as a result of the impossibility for farmers to conciliate forced labour, instated in most colonies in the 19th century under the *Indigénat* rule[28], and work on their own farms. In Oubangui, farmers replaced sorghum by manioc soon after cotton cultivation became compulsory in 1926 (Guillemin, in Tosh 1980), and Geffray (1989) reported a similar switch to manioc cultivation in Mozambique, for the same reason, in the 1940s.

The case of Gabon differs however from the East African situation, as the French stressed little upon expanding cash-cropping, outside timid attempts to develop cacao agriculture, and staked everything on the timber industry. Most of the recurrent problems of food shortages that Gabon has faced throughout the first half of the 20th century hark back to the unrestrained exploitation of okoumé (*Aucoumea klaineana* Pierre, Burseraceae) between 1900 and 1930 (see Bouet 1977, Gray & Ngolet 1999), and to the disruption of farming activities that followed. One of the strongest antagonisms lay in the competition for labour, which was, to a great deal, conditioned by the still clear sexual division of farm labour in Gabon. While planting, weeding, and harvesting are tasks generally and mainly performed by women, men are in charge of clearing and burning forest plots for the preparation of the new farming season. The massive enrolment of men on timber yards resulted in penury of agricultural work force, and led to a generalized famine in Gabon in the 1920s (see Gardinier 1994, Gray & Ngolet 1999, Gray 2002, Bernault 2003). The determination of colonial administrations to foster manioc farming in Central Africa (Jones 1959) in the interwar period largely ensued from this disastrous situation. Colonial agricultural services attempted to palliate the situation by 'modernizing' local agriculture, often with the false idea that food shortages were the result of outmoded farming practices (see Richards 1985 for examples in West Africa). Colonial authorities thus were a direct agent of the spread of manioc farming, and encouraged, sometimes forcibly, the adoption of manioc as a food security crop in most of West and East Africa, but also in parts of Congo, Cameroon, and Gabon (Jones 1959). Manioc reached the present geographical limits of its expansion in Africa (30°N-30°S) under this colonial impulsion (Jones 1959, Cloarec-Heiss & Nougayrol 1998).

[28] The *Code de l'Indigénat* was promulgated by the French government on June, 28th 1881, and applied to all colonies of the French colonial empire. It remained valid until 1946. The British applied a similar policy ("indirect rule") in their colonies.

The depressive effects of labour migrations on African demography and on the general state of local farming in Africa in the first half of the 20th century have been much studied (Sautter 1966, Tosh 1980, Gray 2002, Bernault 2003), but much less is known of the indirect role this past history of manioc in Africa played in the perception that African populations gained on the plant and its agronomy.

### 4.4.2. Linking diversity to history

I chose to explore this question through three examples that I find paradigmatic of manioc diversity in Gabon, and chose to focus on five communities (Odimba, Nombedouma, Douani, Mandilou, and Mbong-Ete), which I present in the following chapters as three case studies of manioc farming in Gabon. These three studies will allow me to examine a number of transversal questions, such as farmers' preferences for bitter or sweet manioc, and their rationale for choosing to maintain a large or limited range of landraces in their farms. It will also provide the material for a wider cross-cultural comparison, in Chapter VI, of variations in perception and valorisation of manioc sexual *versus* clonal reproduction, and their consequences for the dynamics of the genetic diversity of the crop.

# Chapter III

## *"Hitchiking crops in the triangular trade"*

**Odimba**
00°47'28.3"S, 009°09'50.0"E
*Myènè Orungu (B.11b)*

**Nombedouma**
00°55'08.3"S, 010°02'43.4"E
*Myènè Galwa (B.11c)*

## Notes

**1.** Dialectical words are shown in bold.

**2.** Alleles are referred to by the name of the corresponding locus [see Mba *et al.* (2001) and Chavarriaga-Aguirre *et al.* (1998) for the original description of the markers], with their size (expressed in base pairs) specified in subscript.

# Abstract

Manioc introduction in Africa is intimately linked to the development of the transatlantic slave trade on the coast of Africa in the 16th century (Jones 1957, Carter *et al.* 1992). Manioc was first introduced to Africa in 1558 (Carter *et al.* 1992), in São Tomé, in Congo, on the Gold Coast (presently Ghana) and the Slave Coast (presently Togo and Benin), to provision ships bound for Brazil.

When manioc was introduced into Gabon is still a question mark, but evidences concur that support early manioc cultivation among the Myènè, who may have started to grow manioc while slave trade on the coast of Gabon was in full swing, around 1700.

Facing Gabon, in the Bight of Benin, the Portuguese colony of São Tomé played a major role in the regional trade between the 18th and late 19th centuries, and has probably been a major bridge for several American crops to reach the coast of Gabon. Like peanuts (Krapovickas 1969), pumpkins (*Curcubita maxima* Duch. ex Lam., Cucurbitaceae), peas (*Pisum sativum* L., Fabaceae), lemons (*Citrus limon* [L.] Burm. f., Rutaceae), oranges[29] (*Citrus sinensis* [L.] Osbeck, Rutaceae), mangoes (*Mangifera indica* L., Anacardiaceae), papayas (*Carica papaya* L., Caricaceae), tomatoes (*Solanum lycopersicum* L., Solanaceae), cabbage[30] (*Brassica oleracea* L., Brassicaceae), potatoes (*Solanum tuberosum* L., Solanaceae), scallots[31] (*Allium angolense* Bak., Alliaceae), onions, and beans[32]—to name a few—manioc probably "hitchhiked" on boats sailing from São Tomé to Gabon, in the heyday of the slave trade.

Because they were in close trade partnership with São Tomean merchants, the Myènè [B.11] were probably the first population in Gabon to get acquainted with manioc. In this chapter, I focussed on two Myènè tribes, the Orungu [B.11b] and the Galwa [B.11c], showing how their strong involvement in European-African exchanges and their particular connection with São Tomé have probably opened a way for manioc to take root in Gabon, and how this may have been the main stimulus to the re-creation of manioc folk knowledge similar to that of the Amerindians.



[29] See Reynard (1955), Raponda-Walker & Sillans (1962), and Gaulme (1981).

[30] See Vansina (1979).

[31] See Raponda-Walker (1945).

[32] See Raponda-Walker (1952).

# 1. Agambwimbeni n'Itãngani[33]: the Myènè, 1650-1850

From the discovery of the river Gabon by the Portuguese around 1473-1475, to the installation of a French colony in the estuary in 1845, the history of the Myènè [B.10] (Guthrie 1948, Maho 2003) has been tightly enmeshed with that of transatlantic trade on the coast of central Africa. Wary guardians of a trade monopoly with Portuguese, Dutch, Brazilian, and São Tomean merchants calling at Gabon before setting off for Brazil with their cargoes of ebony, ivory, and slaves, the Myènè held the keys to the Ogooué river and to the main accesses to the sea (Map 3.1). Between the 17th and the 19th centuries, they built powerful trade dominions which reached their apogee in the 19th century.



## 1.1. Origins of the Myènè

The origins of most Myènè tribes[34] are lost on the Komo River[35] (Raponda-Walker 1960), and blurred in the multiple versions of oral tradition (see Merlet 1989). Unlike the Mpongwe [B.11a] and the Dyumba [B.11d] who both have a patrilineal descent system, all other Myènè tribes—Galwa, Enenga [B.11f], Orungu and Nkomi [B.11e]—are matrilineal, suggesting that the latter may not be originally Myènè, but offshoots of the Ghisir [B.41] or the Tsogho[36] [B.31], who were 'omyene-ized' (Patterson 1975) as a result of repeated trade contacts with the Mpongwe and the Dyumba (Raponda-Walker 1960, Merlet 1989).

The Mpongwe most likely settled in the estuary between 1375 and 1400[37] (Reynard 1955, Raponda-Walker 1960), while the Dyumba clan* moved further south to Cape Lopez (Patterson 1975). Their presence is attested by Portuguese navigators exploring the coast of Africa in the 15th century (Raponda-Walker 1960).

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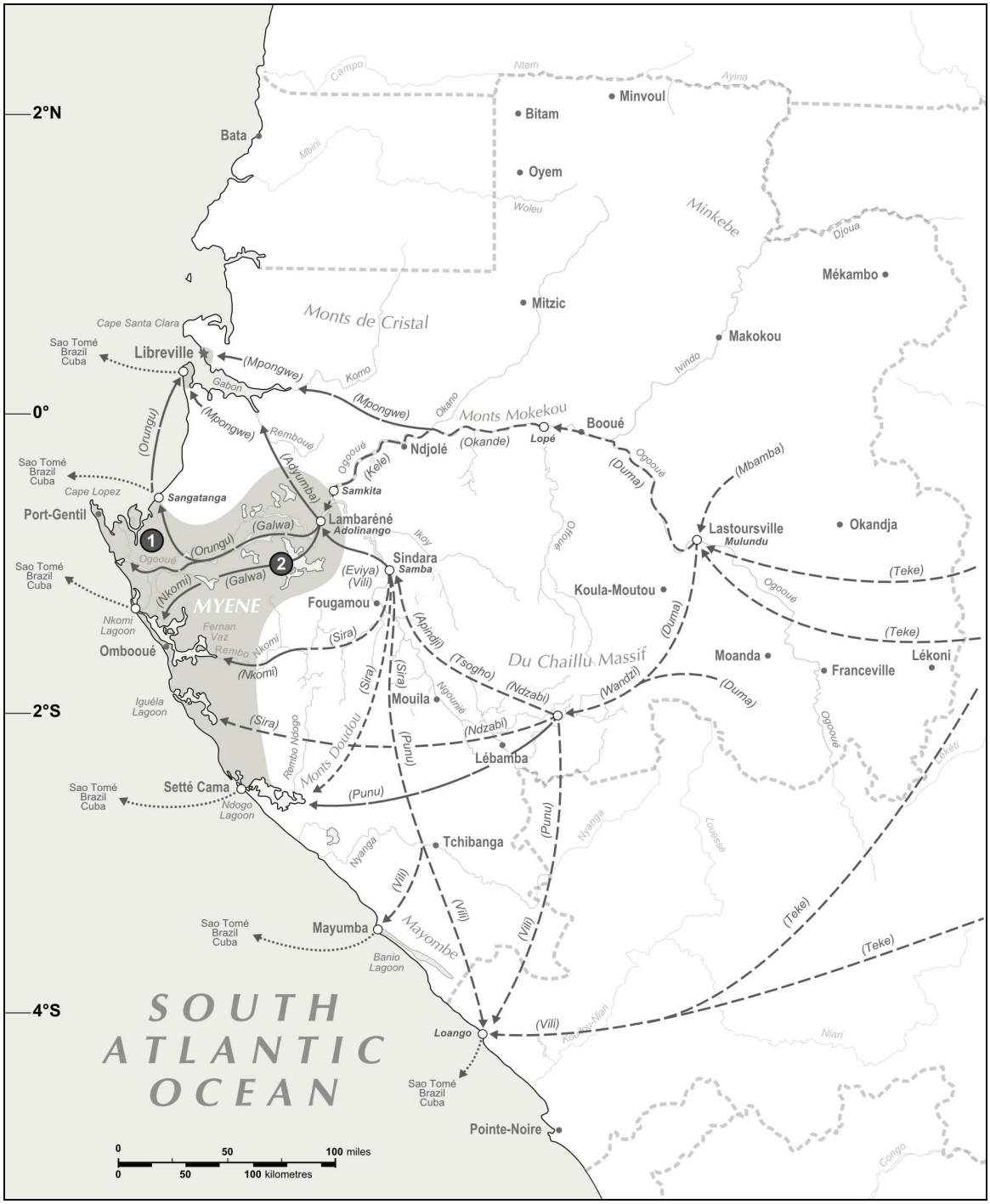
[33] "Masters of the seas", in Myènè.

[34] See Appendix A1 for details on the Myènè linguistic group.

[35] See Merlet (1989) for a review of the different versions of the Myènè migrations in Gabon. Recent linguistic and genetic studies, however, support a common origin in the upper Ngounié with the Tsogho (Van der Veen 2001). The migrations of the Myènè in Gabon are shown in Appendix A2.

[36] Galwa and Enenga, in particular, are believed to be offshoots of the Ghisir (Merlet 1989), while Orungu and Nkomi maintain that they are related to the Tsogho (Gaulme 1981).

[37] Another Myènè tribe, the Ndiwa, probably occupied the estuary before the Mpongwe arrived (Raponda-Walker 1960, Merlet 1989). They were absorbed by the Mpongwe ca. 1700.




**Map 3.1. The Myènè and the riverine trade network in 18th century pre-colonial Gabon**. Trade routes (arrows) formed a complex network of successive tiers of middlemen, partitioning the Ogooué and its tributaries into tribal segments (brackets). Holding the main accesses to the sea, the Myènè channelled all the flow of goods coming from the interior of Gabon (dashed lines). On the coast, Mpongwe and Orungu reserved the right to commerce with European merchants. On the Ogooué, Galwa and Enenga controlled all the traffic downstream, and also tapped the flow of European merchandise moving upstream. At Iguéla, Fernan-Vaz and Setté-Cama, the Nkomi tapped the commerce coming from the Nyanga and from the Teke plateaux. Adapted from Sautter (1966), Merlet (1989) and Gray (2002). The location of Odimba ❶ and Nombedouma ❷ is reported on the map.

In the Ogooué, Galwa and Enenga moved near Lakes Onangué and Oguemoué (Merlet 1989) and the Orungu to Cape Lopez in contact to the Dyumba (Raponda-Walker 1960), while the Nkomi crossed the savannahs of the Ngounié valley to establish at Fernan-Vaz and Setté-Cama (Gaulme 1981). At first, the Galwa probably followed the Orungu in their movement to the coast to reap the fruits of slave trade developing at Cape Lopez, but were stopped at Lake Onangué by the Ghisir (Sautter 1966). In the 17th century, as commerce developed at Cape Lopez, the temptation to challenge the Dyumba monopoly on trade with European merchants grew stronger among the Orungu. Around 1690-1700, the latter wrested control over the bay, and with the support of the Galwa, drove the Dyumba far back inland, casting them away to Lake Azingo (Raponda-Walker 1960, Patterson 1975).



## 1.2. The rise of the Myènè

### 1.2.1. The discovery of Gabon: 1470-1480

Trade on the coast of Gabon dates back to the discovery of São Tomé and Príncipe in 1471. Shortly after, the Portuguese began the systematic exploration of the Atlantic shores of central Africa, and the *Rio do Gabam*, which later became Gabon, appeared for the first time on Portuguese maps around 1485 (Reynard 1955, Patterson 1975, Merlet 1990a). While they developed their colony in São Tomé, Portuguese merchants started to trade regularly on the coast of Gabon, principally at Cape Lopez with the Dyumba, and at Pointe Denis, in the Gabon estuary, with the Mpongwe, drawing detailed maps of the coast by the mid-16th century[38] (Patterson 1975).

Without however taking the proportion of Loango (Merlet 1991), trade developed in Gabon throughout the 16th and 17th centuries as ships called for water and provisions, and to buy dyewood (padouk, *Pterocarpus soyauxii* Taub., Fabaceae) and ivory (Patterson 1975). Around 1630-1640, the Dutch, seeking slaves to supply their colonies in Brazil, evicted the Portuguese from Loango. To thwart the restrictions imposed by the Dutch, the Portuguese started to use Gabon as an alternative supply for slaves, and São Tomé as a depot, where slaves were stashed, awaiting their deportation to Brazil (Patterson 1975).

[38] Several landmarks along the coast of Gabon took their name from Portuguese navigators. Cape Lopez, for example, took its name from Lopo Gonçalvez, and the Fernan-Vaz lagoon was named after Fernão Vaz who discovered it in 1473 (Reynard 1955, 1956).

Masters of the Ogooué delta, the Orungu controlled the only navigable way into Gabon, sharing with the Galwa two key positions in the *courtier* system (Patterson 1975) regulating the commerce along the Ogooué. At Adolinango ("I see the tribes coming", in Myènè), the Galwa watched over the convoys loaded with ivory, ebony, rubber and slaves coming from the Ngounié (Samba) and from the upper Ogooué (Lopé), and received in exchange alcohol, tobacco, gunpowder, and fabrics that the Orungu bartered on the coast with European merchants (Merlet 1989).

### 1.2.2. Heyday of the slave trade in Gabon: 1700-1840

The slow decay of Loango in the 18th century marked an important step in the ascension of the Myènè (Patterson 1975, Merlet 1989). As the political strength of the Vili [H.12] declined, the influence of the Myènè grew stronger. In the 1750s, trade on the coast of Gabon dramatically increased (Patterson 1975). Until then, ivory, wax, ebony and dyewood had been the main items sought in Gabon. However, after 1770, the slave trade began to take new dimensions in Gabon (Merlet 1990a).

With the abolition of slave trade voted by the British parliament in 1807, traffic shifted to smaller and less conspicuous markets, where it could resume out of sight of British sentinels patrolling off the coast of Loango to track down interlopers (Merlet 1989). Between 1809 and 1815, the frequentation of Setté-Cama, Cape Lopez and Pointe Denis increased, and altogether the coast of Gabon exported between 1,000 and 1,500 slaves every year (Patterson 1975).

Buying manufactured goods from European and American ships, São Tomean merchants sailed to Gabon to exchange with the Myènè [B.11] manufactured goods against slaves, which supplied the Cuban and Brazilian markets (Patterson 1975).

### 1.2.3. French Gabon: 1840-1880

From Setté-Cama to Cape Santa-Clara, the coast of Gabon became an endless succession of barracoons[39] (Raponda-Walker 1960, Merlet 1989). Midway between Gabon and Cape Lopez, Sangatanga (from the Myènè **ossèng'atãnga**, "the Whites' rendezvous") became the most important slave market in Gabon (Merlet 1989, Patterson 1975). But while trade flourished at Cape Lopez, it slowly waned in the Gabon estuary.

[39] Shacks (*barraçoes*, in Portuguese) where traders (Brazilians and São Tomeans mostly) held slaves until a ship arrived (Raponda-Walker 1960, Sautter 1966, Merlet 1989).

Since 1840, the French had strengthened their position in the estuary by signing a series of treaties with the local chiefs and opening a *comptoir* at Fort Aumale in 1843, as a way to claim possession of the Gabon (Patterson 1975, Merlet 1989, 1990a). The presence of the French station at Gabon however considerably impeded commerce with São Tomé, and made impossible direct slave exports from Pointe Denis (Patterson 1975).

As the French concentrated their efforts in the estuary, the colonisation at Cape Lopez did not start up until the 1880s, postponing for a while the downfall of the Orungu dominion. The expansion of cocoa and coffee cultivation in São Tomé in the 1860s had temporarily revived a clandestine commerce of slaves with the Portuguese archipelago, but slave trade was sputtering to a close (Patterson 1975).

In 1860, the French started the exploration of the Ogooué from the Fernan-Vaz lagoon, down the Rembo Nkomi, to by-pass the Orungu who forbade them access to the Ogooué (Merlet 1989). They reached the Galwa in 1862, who seized this opportunity to attract factories at Adolinango and trade directly with the **Motãngani**[40]. In 1866, Hatton and Cookson, followed shortly by others (Holt, Woerman), built the first factories at the confluence of the Ogooué and the Ngounié, laying the foundation of Lambaréné (Raponda-Walker 1960).

Although the Galwa profited at first from their new leading position, this prosperity was rather short-lived. Between 1875 and 1878 de Brazza succeeded in opening the Ogooué to European penetration, and factory steamers thrust into the river (Patterson 1975). The products in demand changed[41], and with them also the actors of trade in Gabon.

### 1.2.4. Demise of the Myènè hegemony: 1880-1900

By disrupting the old trading system, the factories opened new opportunities for the populations of the interior, long denied direct access to merchandise and tired of getting only the leftovers of trade. In the second half of the 19th century, the factories established in the French *comptoir* attracted large numbers of Kèlè [B.22], Shekiani [B.21], and particularly Fang[42] [A.75], pushing towards the coast and eventually eclipsing the Mpongwe in the estuary (Patterson 1975, Chamberlin 1978, Merlet 1990a, Bernault 2003).

[40] "The Whites", literally "the ones who pay" (Van der Veen & Bodinga-bwa-Bodinga 2002).

[41] Rubber, starting ca. 1853, and timber, ca. 1900.

[42] See Chapter V.

Important population shifts continued in Gabon throughout the 20th century. In Lambaréné, the new craze in Europe for Gabon timber species, particularly okoumé[43] (*Aucoumea klaineana* Pierre, Burseraceae), lured into the former Galwa dominion thousands of Ghisir [B.41], Punu [B.43], Kèlè, and Fang (Sautter 1966, Gray 2002). In Setté-Cama, the "okoumé fever" also attracted Ghisir, Varama [B.402], Lumbu [B.44] and Vili [B.503], where they mingled with the Nkomi (Gaulme 1981).

## 1.3. Odimba and Nombedouma

In 2006 and 2007, I visited two Myènè communities. The first village I surveyed, Nombedouma (00°55'08.3"S, 010°02'43.4"E), is a community of Galwa fishermen on Lake Onangué, in the Moyen-Ogooué province. The second village I visited, Odimba (00°47'28.3"S, 009°09'50.0"E), is a mixed community Orungu-Punu located near the mouth of the Gangwe river, in the periphery of Port-Gentil.



### 1.3.1. The history of Odimba and Nombedouma

Aside from a fleeting mention of Nombedouma as an important Galwa community in the 1850s (see Raponda-Walker 1960), little is known of the early history of the two communities. Located on the confluence of several routes linking the Ogooué, the Ngounié and the Fernan-Vaz, villages of Lake Onangué like Nombedouma were a dynamic cog in the workings of the riverine trade network throughout the 18th and 19th centuries (Sautter 1966). The Galwa bought ivory, ebony, and slaves from the Vili, the Eviya [B.301] and the Ghisir, and sold them to the Orungu, who conveyed them to the barracoons on the coast.

With the transformation of local economy in the first half of the 20th century, the nature of merchandise changed, but trade activities continued. While Port-Gentil and Lambaréné developed and appealed to large numbers of people, the demand for farming products also increased in the nascent cities, opening new economic prospects for agriculture, which the Myènè disdained in the past (see Patterson 1975). In Odimba, people turned to an economy centred on market gardening, supplying Port-Gentil with manioc and fresh vegetables. In the lakes region, Galwa, Fang and Kèlè similarly organised in complex networks to supply Port-Gentil and Lambaréné with manioc and fish (Sautter 1966). However these networks, Sautter notes, are clearly distinct and

[43] See Chapter IV.

mutually exclusive. In Nombedouma, which Sautter visited in the 1960s, the people specialized in fishing, leaving manioc farming to the Fang of the neighbouring villages (Sautter 1966).

### 1.3.2. Surveys

I visited Nombedouma in October 2006 and Odimba in September 2007. Fourteen farmers, all Galwa, participated in the survey in Nombedouma. In Odimba, I interviewed twelve farmers (four Orungu [B.11b], five Punu [B.43], two Vili [B.503] and one Kèlè [B.22])[44].



[44] The typology of farmers is presented in Appendix B1.

# 2. Agriculture among the Myènè

It is almost impossible to put a date on the arrival of manioc among the Myènè. Early sources do not mention manioc in the Gabon estuary before the mid-19th century (Jones 1959). Nor was manioc noted at Cape Lopez in 1682 (Barbot, from Patterson 1975). However, manioc may have nonetheless been already common by the time the Orungu replaced the Adyumba at Cape Lopez, ca. 1700. In the oral tradition, the Adyumba left Apomandé after they were defeated by the Orungu and retreated to Lake Azingo, taking with them one cutting of banana and one cutting of manioc (Raponda-Walker 1960).

Until the first voyage of Paul du Chaillu to Gabon in 1857, there are no more written accounts from which the history of agriculture among the Myènè can be surmised. In spite of this historical void, it is however almost certain that manioc became increasingly important after 1750 (Rossel 1987), as the slave trade began to flourish and exchanges intensified with São Tomé (Sautter 1966, Patterson 1975, Gaulme 1981).

It seems that manioc farming developed later in the estuary. From all accounts, manioc was not common around Libreville until the second half of the 19th century (Raponda-Walker 1952, Rossel 1987), where it may have been propped up in the 1860s by missionaries and the personnel of the French station at Fort Aumale (see a description from 1856 in Merlet 1990a). When du Chaillu visited the Mpongwe in 1858, pumpkins (*Cucurbita maxima* Duchesne, Cucurbitaceae) were still the main staple (Raponda-Walker 1952).

## 2.1. The Myènè farming system

### 2.1.1. Agricultural calendar

Myènè farmers clear new farms once a year, towards the end of the long dry season. After clearing away bushes and trees in June-July, the Myènè burn their parcels in August and start planting in September (Figure 3.1). Manioc is planted first. A month and a half later, Myènè farmers plant maize. Other plants (taros, yams, aubergines) are planted afterwards. Farms (**ntsaghá**) last up to three years, then are left to fallow (**ôdá**) for five to ten years, until forest (**igá**) has regained.

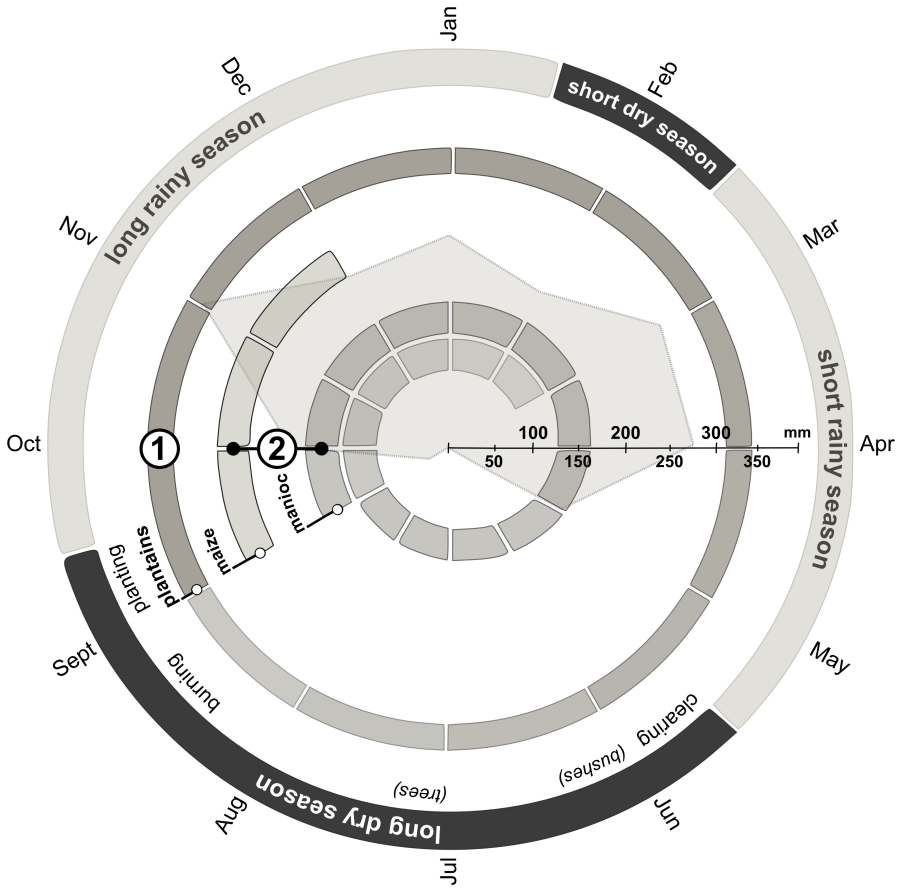



**Figure 3.1. The Myènè agricultural calendar**. Farmers open new farms every year towards the end of the long dry season. Rainfall (radar diagram) demarcates the seasons. While Punu farmers (in Odimba) grow plantains in separate farms (①), Myènè farmers, conversely, intercrop maize, manioc and plantains all in the same farm (②).

In Nombedouma, land available for agriculture in proximity to the village is limited. Farmers open their plantations on the opposite side of Lake Onangué. There, they establish camps (**mpindi**) where they stay for the time they clear or plant new farms. **Mpindi** move with the farms every two-three years, but eventually, farmers have to return to their old plantations.

### 2.1.2. Composition of Myènè farms

Manioc, maize and taros are the three main staples of the Myènè (Table 3.1). All crops are mixed in the farms, but farmers dedicate one area to banana and plantain, and pineapple is planted on the edges to deter wild animals from entering the farm. Maize is harvested after three months, manioc generally after 18 months. Farmers harvest manioc according to their needs, replanting the stem immediately afterwards.

**Table 3.1. Composition of Myènè farms in Odimba and Nombedouma**. Some names are missing. Despite the fact that both speak a common language (omyènè), Orungu and Galwa have different names for several crops. The Galwa actually have the same name for manioc and for maize as the Ghisir (B.41).

| **Crop** | **Latin name** | **Vernacular name** | | **Varieties** |
|---|---|---|---|---|
| | | ***Orungu** (B.11b)* | ***Galwa** (B.11c)* | |
| Atanga | *Dacryodes edulis* | | **Ossegu** | |
| Aubergines | *Solanum* spp. | **Ambolõngo** | **Ambolõngo** | |
| Bananas | *Musa acuminata** | **Atoto** | **Itoto** | |
| Gombo | *Abelmoschus esculentus* | **Inèf** | **Inèfu** | |
| Maize | *Zea mays* | **Issa** | **Putu** | |
| Manioc | *Manihot esculenta* | **Iloti** | **Ghõngo** | |
| Peanuts | *Arachis hypogaea* | **Mbènda** | | 2 varieties |
| Peppers | *Capsicum* spp. | **Togolo** | **Togolo** | |
| Pineapples | *Ananas comosus* | **Ikoko ni atãnga** | **Ighuwu** | |
| Plantains | *Musa sapientum* var. *paradisiaca*** | **Ikõndo** | **Ikõndo** | |
| Pumpkins | *Cucurbita maxima* | **Ilènge** | **Iloghe** | 4 varieties |
| Sorrel | *Hibiscus sabdariffa* | | **Okolo** | |
| Sugar canes | *Saccharum officinarum* | **Ikoko** | **Ikoko** | 3 varieties |
| Spinaches | *Amaranthus* spp. | | | |
| Squashes | *Cucumeropsis mannii* | **Mõndo / Ngõndo** | | 2 varieties |
| Sweet potatoes | *Ipomoea batatas* | **Mõngo** | **Ofoghoza** | 3 varieties |
| Taros | *Colocasia esculenta* | **Ikabu** | **Õnkua** | 2 varieties |
| Tomatoes | *Solanum lycopersicum* | | **Buma** | |
| Yams | *Dioscorea* spp. | **Egwa** | **Imõngo** | 6 varieties |

* AA group; ** ABB group.

## 2.2. Manioc

As in many other villages of the Ogooué-Maritime, manioc farming is central to people in Odimba, who sell a large part of their production in Port-Gentil. Food shortages are common in Port-Gentil, where the soil is unfit for agriculture, and foodstuffs have to be imported from Mouila, Fougamou or Lambaréné[45], or from nearby villages[46]. The average price of manioc *bâtons* in Port-Gentil is usually fivefold that in other parts of the country (Table 3.2). To circumvent this problem, local councils have encouraged farmers' confederations and developed pilot farms to promote local agriculture and supply the markets of Port-Gentil with fresh roots and vegetables.

**Table 3.2. Comparison of standard prices for a bundle of ten bâtons de manioc** in the different provinces of Gabon. As the shape of bâtons varies, so does their weight. On average, a bundle of ten bâtons weighs about 5kg. Prices given in the table are observed prices for this standard quantity of manioc (data from personal observations 2004, 2006, 2007).

| **City / Town** | **Province** | **Price** (in FCFA) |
|---|---|---|
| Libreville | Estuaire | 1,000-2,000 |
| Port-Gentil | Ogooué-Maritime | 4,000-7,000 |
| Lambaréné | Moyen-Ogooué | 2,000 |
| Fougamou | Ngounié | 2,000 |
| Koula-Moutou | Ogooué-Lolo | 2,000 |
| Franceville | Haut-Ogooué | 500-1,000 |
| Bitam | Woleu-Ntem | 750-1,000 |
| Lébamba | Nyanga | 2,000-2,500 |
| Makokou | Ogooué-Ivindo | 1,000-2,000 |

Manioc is a regular source of income for households in Odimba. Each month, women prepare between 40 and 50 bundles of manioc *bâtons*, each of which is sold for around 5,000 FCFA in the market in Port-Gentil. Manioc is also sold as flour (**fariña**). Flour is a highly valued product and is generally saved for the family (see also Sautter 1966). Farmers also sell manioc leaves (200 FCFA a handful), and the "pailles" (**õmpavu**), which they use to wrap manioc into *bâtons* (between 2,000 and 2,500 FCFA the bundle of 50). Bananas, taros, yams and vegetables (aubergines, gombos, and peppers) also complete the range of farming products sent out to Port-Gentil, but manioc brings most of the household income.

[45] I interviewed women in Port-Gentil who bought manioc roots from Lambaréné (16,000 FCFA for ca. 50kg) and prepared manioc *bâtons* (5 to 9 bundles) which they later sold on the market.

[46] See for example Gaulme (1981).

The Galwa of Lake Onangué are traditionally fishermen (Sautter 1966), and grow manioc mainly for subsistence. In Nombedouma, fishing and logging provide most of the income.

### 2.2.1. Planting pattern

Before planting, Myènè farmers notch manioc cuttings (**erere z'ilôti**) to help them take root. Three to five cuttings (the number depending on their diameter) are buried horizontally, and covered with five to ten cm of soil. When planting their farms, Galwa and Orungu mix bitter and sweet landraces. Punu and Vili from Odimba, in contrast, grow bitter and sweet maniocs in two distinct areas.

### 2.2.2. Pests and diseases

Disease prevalence was low in Nombedouma. Half of the farmers I interviewed could not think of any disease and mentioned wild animals (in particular cane rats, *Thryonomys swinderianus* Fitzinger, Thryonomyidae) as the sole pests causing damage to their farms. Rotting of the roots (**ibõng**) was the farmers' main concern. More occasionally, farmers mentioned **abuku**, symptoms of which resemble those of the anthracnose fungus (*Colletotrichum gloeosporioides* Penz.). In any case, the impact of these pathologies was trivial, and farmers were little concerned by the occasional diseases that developed in their farms.

In Odimba, farmers complained about elephants (*Loxodonta cyclotis* Matschie, Elephantidae) and cane rats ravaging their plantations, but most of them (90%) mentioned also a disease which appeared in the village relatively recently (2-3 years) and for which farmers had no name. Again, the symptoms resembled those of anthracnose.

## 2.3. Embedded varietal diversity

I recorded 40[47] names of manioc landraces in Odimba (Table 3.3; 20 corresponding to 'sweet' varieties of manioc, and 20 to 'bitter'), and 46 in Nombedouma (Table 3.4; 13 sweet, 32 bitter, and one undetermined).

[47] Two landraces ('*Marron*', '*Marcelline*') were mentioned to me in the village, but I did not find them afterwards when surveying the farms.

### 2.3.1. Distribution of named diversity

In the two villages, farmers grew on average nine landraces. Farmers in Odimba grew about as many landraces of bitter manioc (**nône**) as of sweet manioc (**ipãndo**), while farmers in Nombedouma grew on average twice as many bitter manioc varieties as sweet varieties. The distribution of landraces among farmers was characterized for the two villages using two evenness indexes, $E_f$ and $E_v$.

*Odimba*

In Odimba, I found $E_f = 0.87$ and $E_v = 0.65$, indicating a relatively constant number of landraces per farmer ($E_f$), but a rather heterogeneous distribution of landraces among farmers ($E_v$). In fact, more than 50% of the names I recorded in the village (21/40) were mentioned only once, while two landraces, '*Matadi*' and '*Lãndi-Lãndi*', were mentioned by 92% of the farmers I interviewed. '*Bakõngo*', '*Madouedoue*', '*Timba Jaune*' and '*Owãntope*' were also among the most popular landraces in Odimba (mentioned by >67% of farmers). Nearly all farmers also grew a few landraces for which they had no name, and to which they referred as "unknowns".

*Nombedouma*

Evenness indexes reflected a similar distribution pattern in Nombedouma ($E_f = 0.87$, $E_v = 0.78$). Only a few landraces were common to more than half of the farmers ('*Okwata*', cited by 71% of the farmers I interviewed, followed by '*Ntse-Putu*', '*Otãngani*', '*Atolizo Ozõmbi*' and '*Premier Choix*'). In contrast, 18 of the 46 names I recorded were cited only once.

**Table 3.3. Distribution of named manioc landraces** (rows) **among farmers** (columns) **in Odimba**. 'x' indicates where the landraces were found. The letters W and P stand respectively for "white" and "purple", in accordance with the colour distinction some farmers made between two types of '*Bakõngo*'.

| **Landraces** | | **RN** | **AH** | **NF** | **ZJ** | **MM** | **IF** | **MF** | **AC** | **MD** | **MC** | **BB** | **MT** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ãmbia N'Idjõmba* | Bitter | | | x | | | | | | | | | |
| *Atolizo Izõmbi* | Sweet | | | | | | | | | | x | | |
| *Bakõngo* † W | Bitter | | | x | | x | x | x | x | | x | | x |
| P | Bitter | | | | | | x | | | | | | x |
| *Belfutu* | Sweet | | x | | | | | | | | | | |
| *Bõndjolãmba* | Sweet | | x | | | | | | | | | | |
| *Bwãnga* | Bitter | | | | | | x | x | | | | | |
| *Côte d'Ivoire* | Sweet | | | | | | x | x | | | x | | |
| *Digõndi* | Bitter | | x | | | | | | | | | | |
| *Edu'u* | Sweet | | x | | | | | | | | | | |
| *Epãndja* | Bitter | x | | | | | | | | x | | | |
| *Francine* | Sweet | | | x | | | | | | | | | |
| *Ibibu* [a] | Bitter | | | | | | | | | | | | x |
| *Iloti Nõmbe* | Sweet | | | | | x | | | | | | | |
| *Inãnga* | Sweet | | x | | | | | | | | | | |
| *Jaune* | Sweet | | | | | | x | | | | | | |
| *Kumba Mavungu* | Sweet | | | x | x | | | | | | x | | |
| *Lãndi-Lãndi* [b] | Bitter | | x | x | x | x | x | x | x | x | x | x | x |
| *Madame Wani* | Bitter | | x | | | | | | x | | | | |
| *Madouedoue* | Sweet | x | | x | x | x | x | x | | x | x | | |
| *Matadi* [c] †,‡ | Sweet | | x | x | x | x | x | x | x | x | x | x | x |
| *Maya* [d] | Bitter | | x | x | | | | | | | | | |
| *Mõngiloti* [e] | Bitter | | | x | | | | | | | | | |
| *Mpira-Nõmbe* | Sweet | | | | x | | | | | | | | |
| *Muwivu* | Bitter | | | | | x | | | | | | | |
| *Ndimina* | Sweet | | | | x | | | | | | | | |
| *Ndzao Re Bimbia* | Bitter | | | | | | x | x | x | | x | x | |
| *Ngwesuku* †,‡ | Bitter | | x | | | | x | | | | | | |
| *Ntselele* | Bitter | | x | | | x | | | | | | x | |
| *Ntsumu* | Bitter | | x | | | | | | | | | | |
| *Ogurungu* [f] | Bitter | | x | x | | | | | | | | | |
| *Okwata* | Sweet | | x | x | | | | x | | | | | |
| *Omboma* | Bitter | | x | | | | | | | | | | |
| *Owãntope* | Bitter | | x | x | x | x | x | x | | x | x | | |
| *Pãndinu* | Sweet | | | | | | | | x | | | | |
| *Pauline* † | Sweet | | | x | x | | | | | | | | |
| *Premier Choix* [g] | Bitter | | x | | | | | | | | | | |
| *Putu* §,†,‡ | Bitter | | x | x | | | | | | | | | |
| *Tambroussi* | Sweet | | | | | | | x | | | | | |
| *Timba Jaune* [h,i] | Sweet | | x | | x | x | x | x | x | | x | x | |

[a] Punu name. [b] Also known as '*Landeuleuleu*' among the Ghisir. [c] Found sometimes as '*Ogelo*'. [d] Also called '*Luanda*'. [e] Synonym of '*Ndzao Re Bimbia*'. The same landrace is also known as '*Oguka*', '*Rizõmbo*', '*Karonari*', '*Ngungu Remba*', and '*Ndjawebimbia*'; [f] Also called '*Pinde*'. [g] Also found as '*Monãnzabe*' among the Tsogho [B.31], the Apindji [B.303], the Pubi [B.304] and the Eviya [B.301]. [h] '*Muguwi*' in Ghisir [B.41]. [i] '*Make Ta Koko*' in Punu [B.43]. § Previously recorded by Raponda-Walker and Sillans (1961). † Recorded by Sautter (1966). ‡ Recorded by Gaulme (1981) among the Nkomi in the Fernan-Vaz.

**Table 3.4. Distribution of named manioc landraces** (rows) **among farmers** (columns) **in Nombedouma**. 'x' indicates where the landraces were found. The letters W and R stand respectively for "white" and "red", in accordance with the colour distinction some farmers made between two types of '*Oghoa*'.

| **Landraces** | | **OMF** | **NJ** | **OM** | **OC** | **AG$_1$** | **NM** | **AA** | **NF** | **AP** | **IL** | **OJ** | **AG$_2$** | **OF** | **IG** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Adyanu* | Sweet | | | | x | | | | | | | | | x | x |
| *Ambaze* | Bitter | | | | | | | | | | | | | x | x |
| *Atolizo-Ozõmbi* | Bitter | | x | | x | | x | | x | | | | | x | x |
| *Ayumbo* † | Bitter | | | | | | | | | | x | | | | |
| *Bakõngo* † | Bitter | x | x | | | | | x | | | | | | x | x |
| *Cécile* | Bitter | | | | | | | | | | | | | x | x |
| *Colette* | Bitter | | | | | x | | | | | x | | | | |
| *Ekolo'Arendo* | Bitter | | | | | | | | | | | | x | | |
| *Esõnge* | Bitter | | | | x | | | | | | | | | | |
| *Evizovizo* † | Sweet | | | | | x | | | | | | | | | |
| *Geneviève* | Bitter | | | | | | | | | | | | | x | x |
| *Idjõmba s'eliwa* | Bitter | | | | | x | | | | | x | | | | |
| *Ighozo* | Bitter | | | x | | | | | | | | | | x | x |
| *Ikolõngo* | Bitter | | | | | | | | | | x | | | | |
| *Ikõndo* | Bitter | | | | | | | | | | | x | | | |
| *Ikwãmba* † | Sweet | | | | | | | | | | | x | | | |
| *Lambarene* | Bitter | | | x | | | | | | x | | | x | | |
| *Lãngalãnga* | ? | | | | | | | | x | | | | | | |
| *Laurence* | Bitter | | | | x | | | | | | | | | x | x |
| *Lingala* | Sweet | | | | | x | | | | | | | | x | x |
| *Loulou* | Bitter | | | | | | | | | | | | | x | x |
| *Matadi* †,‡ | Sweet | x | x | | | | | x | x | | | | | | |
| *Mpiza-Vizue* | Sweet | | | | | | x | x | | | | x | | | |
| *Mpõngwe* | Bitter | | | | | | | | | | | | x | | |
| *Ndina* | Bitter | | | x | | | | | | | | | | | |
| *Ndza-Bouane* | Bitter | | | | | | | | | | | | | x | x |
| *Ngu'u* | Bitter | | | | x | | x | | | | | | x | | |
| *Nkoula-Nõmbe* | Bitter | | | x | | | | | | | | | | x | x |
| *Ntselele* | Bitter | | x | | | | | | x | | | | | | |
| *Ntse-Putu* † | Bitter | x | x | | | | | x | x | | x | | x | x | x |
| *Nzengui* | Sweet | | | | | | | | | x | | | | | |
| *Nzoghou* | Bitter | | | x | x | | | | | | | | | x | x |
| *Oghoa* W | Sweet | | | | | | x | x | | | | x | | | |
| R | Sweet | | | | | | x | | | | | x | | | |
| *Ogulungu* | Sweet | | | x | | | | | | | | x | | x | x |
| *Okwata* | Sweet | x | x | x | x | | x | x | x | | x | | | x | x |
| *Olaloa* | ? | | | | | x | | | | | | | | | |
| *Onindi* | Bitter | | | | x | | | | x | | x | | | | |
| *Ossamouédembo* | Bitter | | | | | | | | | | | | x | | |
| *Ossewa* | Sweet | | | | | | | x | | | | x | | | |
| *Otãngani* | Bitter | x | x | | x | | | | x | | x | | | x | x |
| *Oyogho* † | Bitter | x | | | | | | | | | | | | | |
| *Pauline* † | Sweet | | | | | | | | | | | x | | | |
| *Premier Choix* | Bitter | x | x | | | | | | x | | x | x | | | |
| *Putu-Bakõngo* | Bitter | | | | | | | x | | | | | | | |
| *Regholoto* † | Bitter | | | | | | | | | | x | | | | |
| *Samkita* | Bitter | | | | | | | | | | | | x | | |
| *Tia* | Bitter | | | | | | | | | | | | | x | x |
| *Yabouge* | Bitter | | | | | | | | | | | | x | x | x |

† Recorded by Sautter (1966). ‡ Recorded by Gaulme (1981) among the Nkomi in the Fernan-Vaz.

### 2.3.2. Origin of landraces

Among the Myènè, the transmission of landraces is vertical. Manioc cuttings are traditionally given by mothers to their daughters, but cuttings may also be exchanged with other members of the family. In Nombedouma, all farmers had received their cuttings from relatives. In Odimba, in addition to the landraces they had received from their relatives, all farmers I interviewed grew landraces which had been provided by the local council.

*Odimba*

In Odimba, farmers considered '*Putu*' ("the Portuguese") as the first ever cutting their ancestors were given. Earlier descriptions of the Myènè varietal portfolio attest to the long history of the landrace. '*Putu*' is already mentioned in the 1960s by Sautter (1966) in Nombedouma, and the landrace is also listed by Raponda-Walker and Sillans (1961) among the Mpongwe [B.11a] and the Nkomi [B.11e]. Twenty years later, Gaulme (1981) mentions again '*Putu*' as a popular landrace among the Nkomi in the Fernan-Vaz. Although the tradition is now waning and '*Putu*' has lost ground in favour of '*Matadi*' and '*Lãndi-Lãndi*, Orungu farmers used to plant '*Putu*' before any other manioc landrace or any other crops in their farms.

All farmers in Odimba also grew a few landraces for which they did not have a name ("unknown" landraces). About two-three years ago, the appearance of a new strain of disease, unknown to local populations, seemingly provoked a shortage of planting material in the village, forcing farmers to ask for cuttings or to buy some (2,000 FCFA the bundle) from other villages (Nkendje, Igendja, Bõndjolãmba). Many of the unknown landraces were part of a batch of assorted cuttings donated to farmers by the local council to help them opening new plantations, however without always mentioning the names of the varieties to which the cuttings belonged.

*Nombedouma*

According to farmers' accounts, '*Ntselele*' ("the termite") and '*Ntse-Putu*' ("Portugal") were among the first manioc landraces the Galwa started growing, but ever since, they have accumulated a large diversity of varieties, regularly bringing new cuttings back from neighbouring villages ('*Yamouge*', from a Fang [A.75] village, or '*Ndza-Bouane*', a Kèlè [B.22] landrace).

## 2.4. Manioc volunteers

Two to three times a year, Myènè farmers weed their farms. Farmers in the two villages differentiated manioc volunteers (**ntsumu**, "that which crops up) from the weeds that grew after burning (**owõngo**, "everything that grows"[48]).

### 2.4.1. Densities of volunteers

Densities of manioc volunteers in the farms were high in Nombedouma (Table 3.5) and Odimba (Table 3.6). In the two villages, densities of volunteers were assessed two weeks after farms had been burned, and before planting had started. Hence, although the sample is small in the two villages, the values reflect the high prevalence of manioc volunteers in Myènè farms.



**Table 3.5. Density of volunteer seedlings in Nombedouma**.

| Farms | Density/$m^2$ | Fallow length |
|---|---|---|
| $A_2$ | 2.8 ± 0.9 | 3 years |
| $K_1$ | 0.8 ± 0.5 | 1 year |
| Average | 1.8 ± 1.4 | |

**Table 3.6. Density of volunteer seedlings in Odimba.**

| Farms | Density/$m^2$ | Fallow length |
|---|---|---|
| $C_1$ | 0.9 ± 0.8 | 10 years |
| $D_1$ | 3.0 ± 1.4 | 4 years |
| $E_3$ | 1.2 ± 0.5 | (4-5 years) |
| $I_1$ | 3.0 ± 1.2 | (4-5 years) |
| Average | 2.0 ± 1.2 | |

### 2.4.2. Management of seedlings

Myènè farmers, Galwa and Orungu alike, let manioc volunteers develop in their farms, harvest them, and if the cutting is deemed of some interest (unusual morphological characteristics) they give it a name and multiply it, thereby creating a new landrace (Tables 3.7 and 3.8). The sole formality to which naming manioc self-sown seedlings is compelled is the consultation of other farmers in the village to confirm the 'uniqueness' of the proposed new landrace. The name is left to the discretion of who discovered the volunteer.

[48] Interestingly, the word is also used for "seeds".

This practice was more common in Nombedouma, where I identified 14 landraces with acknowledged origin from seedlings (Table 3.9). In Odimba, farmers confirmed only six similar cases (Table 3.10). There was also some heterogeneity in farmers' behaviours towards seedlings in Odimba. Punu and Vili established in the village discarded volunteers in order to reduce their incidence among manioc cuttings.

All farmers knew manioc volunteers originate from seeds (**olõnda w'iloti**), but only the Punu in Odimba acknowledged manioc volunteers could display a phenotype different from the mother plant. Galwa and Orungu believed those manioc volunteers they could not name to be seeds from landraces grown in older times and lost since. They gave those a name, usually that of the person who discovered the seedling ('*Cécile*', '*Francine*', '*Geneviève*', '*Laurence*'), or named it after the place where the volunteer was found ('*Bõndjolãmba*', '*Ekolo'Arendo*', '*Ossamouédembo*').

**Table 3.7. Landraces grown from manioc volunteers in Nombedouma**.

| Landrace | Etymology of the name | |
|---|---|---|
| *Tia* | Name of the farmer who found the seedling | Bitter |
| *Adyanu* | Name of the farmer who found the seedling | Sweet |
| *Laurence* | Name of the farmer who found the seedling | Bitter |
| *Onindi* | Name of the farmer who found the seedling | Bitter |
| *Colette* | Name of the farmer who found the seedling | Bitter |
| *Idjõmba s'eliwa* | "Wedding from the lake" | Bitter |
| *Nzengi* | Name of the farmer who found the seedling | Sweet |
| *Ayumbo*† | Name of the farmer who found the seedling | Bitter |
| *Pauline*† | Name of the farmer who found the seedling | Sweet |
| *Ossamouédembo* | Name of a village | Bitter |
| *Ekolo'Arendo* | Name of a village | Bitter |
| *Loulou* | Name of the farmer who found the seedling | Bitter |
| *Cécile* | Name of the farmer who found the seedling | Bitter |
| *Geneviève* | Name of the farmer who found the seedling | Bitter |

† Name previously recorded by Sautter (1966).

**Table 3.8. Landraces grown from manioc volunteers in Odimba**.

| Landrace | Etymology of the name | |
|---|---|---|
| *Bõndjolãmba* | Name of a village | Sweet |
| *Edu'u* | "Old camp" | Sweet |
| *Ngwesuku* | Name of the farmer who found the seedling | Bitter |
| *Ntsumu* | Generic name for manioc volunteers | Bitter |
| *Ãmbia N'Idjõmba* | "Wedding's wealth" | Bitter |
| *Francine* | Name of the farmer who found the seedling | Sweet |

**Table 3.9. Farmers' observations and behaviours towards manioc volunteers in Nombedouma**.

| Observations, behaviours | OMF | NJ | OM | IMT | OC | $AG_1$ | IL | NM | AA | NF | OJ | $AG_2$ | OF | IG | Total | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Have noticed volunteers after burning | x | x | x | x | x | x | x | x | x | x | x | x | x | x | 14 | *100.0* |
| Volunteers originate from seeds | x | x | x | | x | x | x | x | x | x | x | x | x | x | 13 | *92.9* |
| Allow volunteers to grow | x | x | x | x | x | | x | x | x | x | x | x | x | x | 13 | *92.9* |
| *Known landraces* | x | x | x§ | | x§ | | | | | x | x | x§ | | | 7 | *50.0* |
| *Unknown landraces* | | | x§ | | x§ | | | | | | | x§ | | | 3 | *21.4* |
| *Give a name* | | | x† | | x | | | | | | | x | x | x | 5 | *35.7* |
| *Do not give a name* | | | | | | | | | | | | | | | 0 | *0.0* |
| Thin volunteers out | x | x | x | | x | | | | | | | | | | 4 | *28.6* |

§ May recognize some volunteers but not all of them.
† '*Tia*' was a landrace named after her grandmother who found the volunteer.

**Table 3.10. Farmers' observations and behaviours towards manioc volunteers in Odimba**.

| **Observations, behaviours** | **RN** | **AH** | **NF** | **ZJ** | **MM** | **IF** | **MF** | **AC** | **MD** | **MC** | **BB** | **MT** | **Total** | **%** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Have noticed volunteers after burning | x | x | x | x | x | x | x | x | x | x | x | x | 12 | *100.0* |
| Volunteers originate from seeds | x | x | x | x | x | x | x | x | x | x | x | x | 12 | *100.0* |
| *Same as mother plant* | | | | | | | x | | | | | | 1 | *8.3* |
| *Different from mother plant* | | | | | | x | | | x | x | x | x | 5 | *41.7* |
| Allow volunteers to grow | x | x | x | x | | | | | x | x | x | x | 8 | *66.7* |
| *Known landraces* | x§ | | x§ | x§ | | | | | x§ | | | | 4 | *33.3* |
| *Unknown landraces* | x§ | x | x§ | x§ | | x | x | | x§ | | | | 7 | *58.3* |
| *Give a name* | | x† | x‡ | | | | | | | | | | 2 | *16.7* |
| *Do not give a name* | x | | | x | | | | | x | | | | 3 | *25.0* |
| Thin volunteers out | | | | | x | | x | x | | | | | 3 | *25.0* |
| Discard all volunteers | | | | | | x | | | | | | | 1 | *8.3* |
| *Impede growth of cuttings* | | | | | | x | | | | | | | 1 | *8.3* |

§ May recognize some volunteers but not all of them.
† Gives a name if the volunteer is deemed of interest.
‡ Gave a *ntsumu* her first name, '*Francine*'.

## 2.5. Sampling strategy

In Odimba, 21 landraces (13 bitter and 8 sweet) were sampled (Table 3.11) and genotyped. For each landrace, five plants per landrace and per farmer were collected. Samples were collected over 10 farms. The contribution of each farmer to the sample is shown in Figure 3.2.

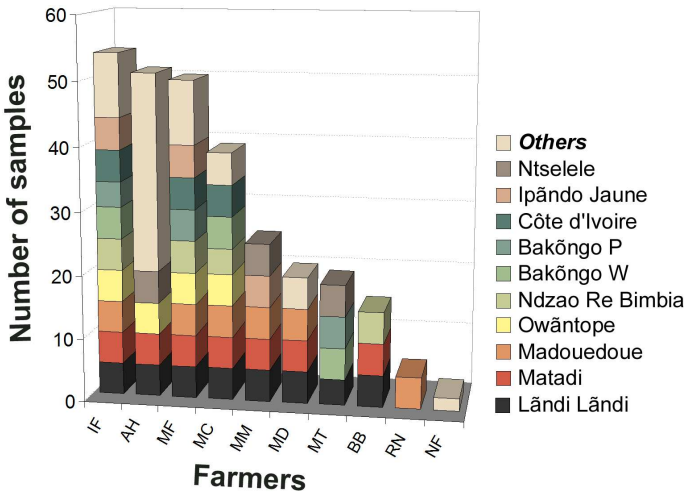



**Figure 3.2. Respective contribution of the ten farmers in Odimba to the total sample** (in order of decreasing importance). Details are given only for the ten most common landraces. Other landraces were grouped into one single category (***others***).

In Nombedouma, five samples, each collected from a different field (13 fields in total), were collected for the five most popular landraces (all bitter). Only one sample could be collected for each of the other 41 landraces (Table 3.12). While I am aware of the limitations of this sampling strategy, the quality of data strongly depends on people's willingness to participate in the study, and data collection was restricted by difficulties encountered while working in Nombedouma. Given, however, the novelty of the practices witnessed there, I chose to make use of all the data at my disposal on manioc among the Myènè, and present data from the two communities.

**Table 3.11. Composition of the data set for Odimba**. The table indicates the number of plants genotyped for each landrace (*N*) and the number of farms from which the samples were collected ($N_F$). The table also gives the frequency of the landraces amongst farmers (popularity) and their prevalence (frequency) in the farms. W and P stand for "white" and "purple", respectively, in accordance with the colour distinction made by farmers between the different morphotypes of '*Bakõngo*'.

| | | | | **Popularity (%)** |
|---|---|---|---|---|
| **Landrace** | | ***N*** | ***$N_F$*** | ***N=12*** |
| *Atolizo Izõmbi* | Sweet | 5 | 1 | *8.3* |
| *Bakõngo* W | Bitter | 14 | 3 | *75.0** |
| P | Bitter | 15 | 3 | — |
| *Bõndjolãmba* ¢ | Sweet | 4 | 1 | *8.3* |
| *Bwãnga* | Bitter | 10 | 2 | *16.7* |
| *Côte d'Ivoire* | Sweet | 15 | 3 | *25.0* |
| *Digõndi* | Bitter | 5 | 1 | *8.3* |
| *Epãndja* | Bitter | 5 | 1 | *16.7* |
| *Ipãndo Jaune* | Sweet | 15 | 3 | *66.7* |
| *Lãndi-Lãndi* | Bitter | 39 | 8 | *91.7* |
| *Madame Wani* | Bitter | 5 | 1 | *16.7* |
| *Madouedoue* | Sweet | 30 | 6 | *66.7* |
| *Matadi* | Sweet | 35 | 7 | *91.7* |
| *Ndzao Re Bimbia* | Bitter | 19 | 4 | *41.7* |
| *Ngwesuku* | Bitter | 10 | 2 | *16.7* |
| *Ntselele* | Bitter | 15 | 3 | *25.0* |
| *Ogurungu* | Bitter | 5 | 1 | *16.7* |
| *Okwata* | Sweet | 5 | 1 | *25.0* |
| *Owãntope* | Bitter | 20 | 4 | *66.7* |
| *Premier Choix* | Bitter | 4 | 1 | *8.3* |
| *Totomavemi* | Sweet | 5 | 1 | *8.3* |
| Total | | 280 | | |

* Both morphotypes combined; ¢ Landrace grown from seedling.

**Table 3.12. Composition of the data set for Nombedouma**. Y and R stand for "yellow" and "red", respectively, in accordance with the colour distinction made by farmers between the different morphotypes of '*Oghoa*'.

| | | | | Popularity (%) |
|---|---|---|---|---|
| **Landrace** | | ***N*** | ***$N_F$*** | ***N=14*** |
| *Atolizo-Ozõmbi* | Bitter | 5 | 5 | *42.9* |
| *Ntse-Putu* | Bitter | 5 | 5 | *57.1* |
| *Okwata* | Bitter | 5 | 5 | *71.4* |
| *Otãngani* | Bitter | 5 | 5 | *50.0* |
| *Premier Choix* | Bitter | 5 | 5 | *35.7* |
| *Adyanu* | Sweet | 1 | 1 | *21,4* |
| *Ãmbaze* | Bitter | 1 | 1 | *14,3* |
| *Ayumbo* | Bitter | 1 | 1 | *7,1* |
| *Bakõngo* | Bitter | 1 | 1 | *35,7* |
| *Cécile* | Bitter | 1 | 1 | *14,3* |
| *Colette* | Bitter | 1 | 1 | *14,3* |
| *Ekolo'Arendo* | Bitter | 1 | 1 | *7,1* |
| *Esonge* | Bitter | 1 | 1 | *7,1* |
| *Evizovizo* | Sweet | 1 | 1 | *7,1* |
| *Geneviève* | Bitter | 1 | 1 | *14,3* |
| *Idjomba s'eliwa* | Bitter | 1 | 1 | *14,3* |
| *Ighozo* | Bitter | 1 | 1 | *21,4* |
| *Ikolõngo* | Bitter | 1 | 1 | *7,1* |
| *Ikõndo* | Bitter | 1 | 1 | *7,1* |
| *Ikwãmba* | Sweet | 1 | 1 | *7,1* |
| *Lambarene* | Bitter | 1 | 1 | *21,4* |
| *Lãnga Lãnga* | ? | 1 | 1 | *7,1* |
| *Laurence* | Bitter | 1 | 1 | *21,4* |
| *Lingala* | Sweet | 1 | 1 | *21,4* |
| *Loulou* | Bitter | 1 | 1 | *14,3* |
| *Matadi* | Sweet | 1 | 1 | *28,6* |
| *Mpiza-Vizue* | Sweet | 1 | 1 | *21,4* |
| *Mpõngwe* | Bitter | 1 | 1 | *7,1* |
| *Ndina* | Bitter | 1 | 1 | *7,1* |
| *Ndza-Bouane* | Bitter | 1 | 1 | *14,3* |
| *Ngu'u* | Bitter | 1 | 1 | *21,4* |
| *Nkoula-Nombe* | Bitter | 1 | 1 | *21,4* |
| *Ntselele* | Bitter | 1 | 1 | *14,3* |
| *Nzengui* | Sweet | 1 | 1 | *7,1* |
| *Nzoghou* | Bitter | 1 | 1 | *28,6* |
| *Oghoa* Y | Sweet | 1 | 1 | *21,4* |
| R | Sweet | 1 | 1 | *14,3* |
| *Ogulungu* | Sweet | 1 | 1 | *28,6* |
| *Ossamouédembo* | Bitter | 1 | 1 | *7,1* |
| *Ossewa* | Sweet | 1 | 1 | *14,3* |
| *Pauline* | Sweet | 1 | 1 | *7,1* |
| *Putu-Bacongo* | Bitter | 1 | 1 | *7,1* |
| *Regholoto* | Bitter | 1 | 1 | *7,1* |
| *Samkita* | Bitter | 1 | 1 | *7,1* |
| *Tia* | Bitter | 1 | 1 | *14,3* |
| *Yabouge* | Bitter | 1 | 1 | *21,4* |
| Total | | 66 | | |

# 3. Genetic diversity in Myènè farms

## 3.1. Structure of genotypic diversity in Odimba

Genotypic diversity was analyzed over 280 samples. In total, I identified 26 multilocus genotypes[49] (arbitrarily numbered G1 to G26), 23 of which were specific to one landrace (Table 3.13). Three MLGs (G1, G6, and G25) were shared by different landraces. I also found 19 plants with atypical genotypes (singletons*, a third of which I had collected over a single farm.

### 3.1.1. Genotypic characterization of landraces

Eight out of the 21 landraces analyzed (38.1%) were strictly monoclonal, and five (23.8%) consisted of one clone but included also a few singletons (Table 3.14). Even among the polyclonal landraces (‘*Bakõngo*’ W, ‘*Ntselele*’, ‘*Ngwesuku*’), each of the different clones I identified was grown by a different farmer, but I never found the same clone in more than one farm, or more than one clone for a given landrace in a single farm. In fact, 16 of the 26 MLGs I identified were grown by one single farmer.

The analyses confirmed one case of synonymy (‘*Ndzao Re Bimbia*’ and ‘*Digõndi*’, both G25), and suggested another one (‘*Owãntope*’ and ‘*Lãndi-Lãndi*’, G1 and G6). Farmers were aware of the first case and had mentioned the two names as referring to the same landrace. In contrast, all farmers treated ‘*Owãntope*’ and ‘*Lãndi-Lãndi*’ as two distinct varieties, but the distinction seemed rather loose. G1 was predominantly found in ‘*Lãndi-Lãndi*’ and G6 in ‘*Owãntope*’, but plants labelled ‘*Owãntope*’ were often genotypically confounded with plants of ‘*Lãndi-Lãndi*’, and conversely.

### 3.1.2. Indexes of agreement

On the whole, landraces formed homogeneous (average consistency index, $C_F = 93.5\% \pm 8.4$) and harmonious genetic entities (average index of agreement, $OA_j = 93.7\% \pm 6.6$, ranging from 82.5% for farmer AH to 100% for RN; 98 comparisons). Only four plants were clearly misidentified by farmers.

[49] Subsequently abbreviated MLG.

**Table 3.13. Allelic composition of the 26 MLGs and 19 singletons identified in Odimba** at each of the ten loci studied. The corresponding landrace is also indicated. Alleles are coded with numbers, with the numbers referring to the allele's size (in base pairs) by increasing order*.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| G1 | *Lãndi Lãndi* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/2 | 6/7 | 3/3 | 2/2 | 3/3 |
| G2 | *Atolizo Izõmbi* | 1/1 | 1/1 | 2/3 | 2/5 | 1/2 | 2/2 | 5/7 | 5/5 | 2/9 | 1/3 |
| G3 | *Bakõngo* W | 1/1 | 1/1 | 2/2 | 2/5 | 2/2 | 2/4 | 4/7 | 2/3 | 2/5 | 3/3 |
| G4 | *Ngwesuku* | 1/1 | 1/1 | 2/3 | 1/1 | 1/2 | 3/4 | 1/4 | 2/3 | 6/6 | 3/3 |
| G5 | *Ndzao Re Bimbia* | 1/1 | 1/1 | 2/3 | 1/2 | 2/2 | 2/4 | 6/7 | 3/3 | 4/9 | 3/3 |
| G6 | *Owãntope* | 1/1 | 1/1 | 2/3 | 1/5 | 1/2 | 2/4 | 4/5 | 2/5 | 4/5 | 3/3 |
| G7 | *Ntselele* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 6/7 | 3/5 | 2/6 | 2/3 |
| G8 | *Bwãnga* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 3/4 | 4/5 | 2/5 | 5/6 | 2/3 |
| G9 | *Ngwesuku* | 1/1 | 1/1 | 2/3 | 2/6 | 2/2 | 4/4 | 7/7 | 2/2 | 1/2 | 1/3 |
| G10 | *Ntselele* | 1/1 | 1/1 | 3/3 | 1/2 | 2/2 | 2/4 | 1/6 | 5/5 | 2/6 | 1/3 |
| G11 | *Ntselele* | 1/1 | 1/1 | 3/3 | 1/1 | 1/2 | 2/4 | 3/7 | 2/5 | 5/6 | 3/3 |
| G12 | *Totomavemi* | 1/1 | 1/1 | 3/3 | 2/6 | 1/2 | 2/2 | 7/7 | 2/3 | 9/9 | 3/3 |
| G13 | *Bakõngo* P | 1/1 | 1/3 | 2/4 | 1/5 | 1/1 | 3/4 | 1/4 | 2/3 | 5/8 | 3/3 |
| G14 | *Okwata* | 1/2 | 1/1 | 2/2 | 5/6 | 2/2 | 2/2 | 3/7 | 2/3 | 4/9 | 3/3 |
| G15 | *Madouedoue* | 1/2 | 1/1 | 2/3 | 2/6 | 1/2 | 2/2 | 6/7 | 2/3 | 9/9 | 3/3 |
| G16 | *Ipãndo Jaune* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 3/4 | 1/2 | 3/5 | 2/5 | 3/3 |
| G17 | *Madame Wani* | 1/2 | 1/1 | 3/3 | 2/4 | 2/2 | 2/3 | 1/3 | 3/5 | 7/9 | 2/3 |
| G18 | *Epãndja* | 1/2 | 1/1 | 2/3 | 1/2 | 2/2 | 2/4 | 6/7 | 3/3 | 5/9 | 2/3 |
| G19 | *Bõndjolãmba* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 6/7 | 3/3 | 6/9 | 3/3 |
| G20 | *Matadi* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| G21 | *Premier Choix* | 1/2 | 1/1 | 2/3 | 5/6 | 1/2 | 2/4 | 5/7 | 2/3 | 5/8 | 3/3 |
| G22 | *Madouedoue* | 1/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/3 | 1/5 | 3/5 | 2/4 | 3/3 |
| G23 | *Bakõngo* W | 1/2 | 1/1 | 3/3 | 1/6 | 1/2 | 3/4 | 1/5 | 2/3 | 3/8 | 3/3 |
| G24 | *Côte d'Ivoire* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 2/9 | 3/3 |
| G25 | *Digõndi* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| G26 | *Bakõngo* W | 2/2 | 1/3 | 2/3 | 5/5 | 2/2 | 2/4 | 5/7 | 2/5 | 5/9 | 3/3 |
| 1 | *Atolizo Izõmbi* | 1/1 | 1/1 | 2/2 | 5/5 | 1/2 | 2/4 | 4/7 | 5/5 | 2/4 | 1/3 |
| 2 | *Atolizo Izõmbi* | 1/2 | 1/1 | 2/3 | 2/5 | 1/2 | 2/2 | 5/7 | 3/5 | 2/9 | 3/3 |
| 3 | *Bõndjolãmba* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/3 | 1/1 | 5/6 | 2/3 | 3/3 |
| 4 | *Digondi* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/5 | 3/5 | 6/9 | 3/3 |
| 5 | *Epãndja* | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/4 | 3/6 | 5/5 | 7/9 | 2/3 |
| 6 | *Epãndja* | 1/2 | 1/1 | 2/3 | 2/6 | 1/2 | 2/4 | 6/7 | 3/3 | 5/9 | 2/3 |
| 7 | *Lãndi Lãndi* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 5/7 | 3/3 | 2/2 | 2/3 |
| 8 | *Lãndi Lãndi* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/2 | 6/7 | 3/3 | 6/9 | 3/3 |
| 9 | *Lãndi Lãndi* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 5/7 | 3/3 | 6/9 | 2/3 |
| 10 | *Lãndi Lãndi* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/2 | 5/6 | 3/3 | 2/2 | 3/3 |
| 11 | *Lãndi Lãndi* | 2/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/1 | 3/6 | 6/6 | 3/3 |
| 12 | *Madouedoue* | 1/1 | 1/1 | 2/3 | 1/2 | 2/2 | 2/2 | 3/8 | 3/3 | 2/4 | 3/3 |
| 13 | *Madouedoue* | 1/2 | 1/1 | 2/3 | 2/5 | 1/2 | 2/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| 14 | *Madouedoue* | 1/2 | 1/1 | 2/3 | 2/6 | 2/2 | 2/2 | 6/7 | 2/3 | 9/9 | 3/3 |
| 15 | *Matadi* | 1/1 | 1/1 | 2/3 | 1/2 | 2/2 | 2/2 | 3/7 | 3/3 | 2/4 | 3/3 |
| 16 | *Ndzao Re Bimbia* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/5 | 3/6 | 2/9 | 3/3 |
| 17 | *Ndzao Re Bimbia* | 1/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| 18 | *Ntselele* | 1/1 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 6/7 | 3/5 | 2/6 | 1/3 |
| 19 | *Ogurungu* | 1/1 | 1/3 | 2/4 | 5/5 | 1/1 | 3/4 | 1/4 | 2/3 | 5/8 | 3/3 |

* Corresponding sizes are given in Appendix C3.

**Table 3.14. Genotypic composition of landraces in Odimba**. Genotypes were grouped into 'typical', 'non-typical' and 'atypical' categories, according to their distribution amongst landraces. Typical genotypes were either 'specific' when restricted to one landrace, or 'shared' in the case of synonymies. Corresponding number of individuals are also indicated. Consistency of identifications amongst farmers, $C_F$, was calculated for all landraces (except those that were sampled only from one farm) as the percentage of plants assigned to a given landrace and displaying a MLG typical (specific or shared) of that landrace. Mislabelled plants are reported in the 'mistaken' column.

| **Landraces** | | ***N*** | **Typical** | | **Non-typical** | **Atypical** | **Mistaken** | **$C_F$ (%)** |
|---|---|---|---|---|---|---|---|---|
| | | | **Specific** | **Shared** | | | | |
| *Atolizo Izõmbi* | Sweet | 5 | G2 (3) | — | — | 2 | — | — |
| *Bakõngo* W | Bitter | 15 | G3 (5), G23 | — | — | — | — | *100.0* |
| *Bakõngo* P | Bitter | 14 | G13 (14) | — | — | — | — | *100.0* |
| *Bõndjolãmba* | Sweet | 4 | G19 (3) | — | — | 1 | — | — |
| *Bwãnga* | Bitter | 10 | G8 (10) | — | — | — | — | *100.0* |
| *Côte d'Ivoire* | Sweet | 15 | G24 (15) | — | — | — | — | *100.0* |
| *Epãndja* | Bitter | 5 | G18 (3) | — | — | 2 | — | — |
| *Ipãndo Jaune* | Bitter | 15 | G16 (15) | — | — | — | — | *100.0* |
| *Lãndi-Lãndi* | Sweet | 39 | G1 (32) | — | — | 5 | G6 (2) | *82.1* |
| *Madame Wani* | Bitter | 5 | G17 (5) | — | — | — | — | — |
| *Madouedoue* | Bitter | 30 | G15 (26), | — | — | 2 | — | *93.3* |
| *Matadi* | Sweet | 35 | G20 (34) | — | — | 1 | — | *97.1* |
| *Ndzao Re Bimbia* | Sweet | 19 | G5 (2) | G25 (14) | — | 2 | G24 (1) | *84.2* |
| *syn. Digõndi* | Bitter | 5 | — | G25 (5) | — | — | — | — |
| *Ngwesuku* | Bitter | 10 | G4 (5), G9 | — | — | — | G1 (1) | *90.0* |
| *Ntselele* | Bitter | 15 | G7 (2), G10 | — | — | 1 | — | *93.3* |
| *Ogurungu* | Bitter | 5 | — | — | — | 3 | G13 (2) | — |
| *Okwata* | Sweet | 5 | G14 (5) | — | — | — | — | — |
| *Owãntope* | Bitter | 20 | — | G6 (15) | — | — | G1 (5) | *75.0* |
| *Premier Choix* | Bitter | 4 | G21 (4) | — | — | — | — | — |
| *Totomavemi* | Sweet | 5 | G12 (5) | — | — | — | — | — |

## 3.2. Allelic diversity

Allelic diversity in Odimba was low (average over the landraces, $A_R = 1.859 \pm 0.274$). One allele, $SSR31_{168}$, was private to '*Ipãndo Jaune*'. Five rare alleles (frequency <1%) were also detected, among them $SSR68_{256}$, $SSR68_{266}$, $SSR68_{246}$ (private to '*Ngwesuku*'), $GA126_{193}$ (private to '*Madame Wani*'), and $SSR31_{198}$ (found in only one copy, in '*Madouedoue*').

## 3.3. Overview of genetic diversity in Odimba

Table 3.15 shows the values of pairwise differentiation among 12 of the landraces collected in Odimba ($N_C \geq 10$ only). All landraces were highly differentiated ($F_{ST} = 0.342 \pm 0.108$), with $F_{ST}$ values ranging from 0.115 ('*Bakõngo*' W *vs.* '*Owãntope*'), to 0.580 ('*Bakõngo*' P *vs.* '*Lãndi-Lãndi*'). '*Owãntope*' and '*Lãndi-Lãndi*' were highly differentiated ($F_{ST} = 0.273$, $P < 0.01$). The two morphotypes of '*Bakõngo*' (W and P) were likewise clearly differentiated ($F_{ST} = 0.285$, $P < 0.01$).

Different diversity indexes were also computed for each landrace (Table 3.16). All landraces were characterized by excess of heterozygotes (average $F_{IS} = -0.681 \pm 0.309$), except '*Lãndi-Lãndi*' and '*Ngwesuku*', in which genotype frequencies did not significantly deviate from Hardy-Weinberg equilibrium (Fisher exact test). Genotypic diversity ($R$) was very low (average $R = 0.082 \pm 0.078$).

## 3.4. Overview of genetic diversity in Nombedouma

Genotypic diversity in Nombedouma was high (average over the landraces, $R = 0.750 \pm 0.177$, Table 3.17). In a total of 66 plants, I found 50 distinct multilocus genotypes. Despite the limited number of samples analyzed, allelic diversity in Nombedouma was higher than in Odimba (average over the landraces, $A_R = 2.8 \pm 0.3$). The difference between the two villages was significant (Wilcoxon signed-rank test, $W = 59$, $n_1 = 5$, $n_2 = 12$, $P < 0.01$).

**Table 3.15. Pairwise genetic differentiation ($F_{ST}$) among 14 Orungu landraces** (upper-right matrix), and their significance level (lower-left matrix, Benjamini and Hochberg's sharpened test). ** *P*-value <0.01 Only landraces for which $N_C \geq 10$ were considered.

| | *Bakõngo W* | *Bakõngo P* | *Bwãnga* | *Côte d'Ivoire* | *Ipãndo Jaune* | *Lãndi-Lãndi* | *Madouedoue* | *Matadi* | *Ndzao Re Bimbia* | *Ngwesuku* | *Ntselele* | *Owãntope* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bakõngo W* | | 0.285 | 0.183 | 0.247 | 0.312 | 0.336 | 0.246 | 0.193 | 0.188 | 0.142 | 0.206 | 0.115 |
| *Bakõngo P* | ** | | 0.403 | 0.500 | 0.557 | 0.580 | 0.502 | 0.512 | 0.483 | 0.326 | 0.432 | 0.309 |
| *Bwãnga* | ** | ** | | 0.448 | 0.421 | 0.495 | 0.466 | 0.427 | 0.360 | 0.198 | 0.232 | 0.187 |
| *Côte d'Ivoire* | ** | ** | ** | | 0.429 | 0.415 | 0.333 | 0.258 | 0.299 | 0.389 | 0.387 | 0.358 |
| *Ipãndo Jaune* | ** | ** | ** | ** | | 0.470 | 0.478 | 0.435 | 0.427 | 0.387 | 0.337 | 0.350 |
| *Lãndi-Lãndi* | ** | ** | ** | ** | ** | | 0.359 | 0.290 | 0.455 | 0.426 | 0.382 | 0.273 |
| *Madouedoue* | ** | ** | ** | ** | ** | ** | | 0.238 | 0.395 | 0.362 | 0.381 | 0.301 |
| *Matadi* | ** | ** | ** | ** | ** | ** | ** | | 0.292 | 0.378 | 0.303 | 0.279 |
| *Ndzao Re Bimbia* | ** | ** | ** | ** | ** | ** | ** | ** | | 0.316 | 0.254 | 0.294 |
| *Ngwesuku* | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.174 | 0.192 |
| *Ntselele* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.184 |
| *Owãntope* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | |

**Table 3.16. Overview of genetic diversity in Odimba**, after correction for assignment errors (*Nc*). The table shows the number of distinct genotypes in each landrace (*G*), observed ($H_O$) and expected ($H_E$) heterozygosity, $F_{IS}$, allelic richness ($A_R$, averaged over the loci), private alleles ($A_p$), and an index of clonal richness (*R*). All landraces for which $N_C \geq 5$ were considered.

| Landrace | $N_C$ | $G$ | $H_O$ | $H_E$ | $F_{IS}$ | $A_R$ | $A_p$ | $R$ |
|---|---|---|---|---|---|---|---|---|
| *Atolizo Izõmbi* | 5 | 3 | 0.620 | 0.382 | -0.550** | 1.9 | — | 0.500 |
| *Bakõngo* W | 14 | 1 | 0.667 | 0.528 | -0.231** | 2.5 | — | 0.000 |
| P | 15 | 3 | 0.700 | 0.350 | -1.000** | 1.7 | — | 0.143 |
| *Bwãnga* | 10 | 1 | 0.800 | 0.400 | -1.000** | 1.8 | — | 0.000 |
| *Côte d'Ivoire* | 15 | 1 | 0.700 | 0.350 | -1.000** | 1.7 | — | 0.000 |
| *Digõndi* | 5 | 1 | 0.600 | 0.300 | -1.000** | 1.6 | — | 0.000 |
| *Ipãndo Jaune* | 15 | 1 | 0.500 | 0.250 | -1.000** | 1.5 | $SSR31_{168}$ | 0.000 |
| *Lãndi-Lãndi* | 39 | 7 | 0.349 | 0.239 | -0.445 *NS* | 1.6 | — | 0.158 |
| *Madame Wani* | 5 | 1 | 0.700 | 0.350 | -1.000** | 1.7 | $GA126_{193}$ | 0.000 |
| *Madouedoue* | 30 | 4 | 0.603 | 0.363 | -0.654** | 1.8 | $SSR31_{198}$ | 0.103 |
| *Matadi* | 35 | 2 | 0.691 | 0.354 | -0.952** | 1.7 | — | 0.029 |
| *Ndzao Re Bimbia* | 18 | 4 | 0.600 | 0.300 | -0.732** | 1.8 | — | 0.176 |
| *Ngwesuku* | 10 | 2 | 0.556 | 0.438 | -0.212 *NS* | 2.1 | $SSR68_{246}$ | 0.111 |
| *Ntselele* | 15 | 4 | 0.607 | 0.414 | -0.436** | 2.1 | — | 0.214 |
| *Okwata* | 5 | 1 | 0.500 | 0.250 | -1.000** | 1.5 | — | 0.000 |
| *Owãntope* | 20 | 2 | 0.675 | 0.441 | -0.513** | 2.0 | — | 0.053 |

*NS* Not significant, ** *P*-value < 0.01.



**Table 3.17. Overview of genetic diversity in Nombedouma**. The table indicates the number of plants genotyped for each landrace (*N*) as well as the number of farms from which samples were collected ($N_F$). The table shows the number of distinct genotypes in each landrace (*G*), observed ($H_O$) and expected ($H_E$) heterozygosity, $F_{IS}$, allelic richness ($A_R$, averaged over the loci), and an index of clonal richness (*R*). All landraces for which $N_C \geq 5$ were considered.

| Landrace | $N$ | $N_F$ | $G$ | $H_O$ | $H_E$ | $F_{IS}$ | $A_R$ | $R$ |
|---|---|---|---|---|---|---|---|---|
| *Atolizo Ozõmbi* | 5 | 5 | 3 | 0.820 | 0.542 | -0.426** | 2.8 | 0.500 |
| *Ntse-Putu* | 5 | 5 | 5 | 0.480 | 0.512 | 0.172 *NS* | 2.6 | 1.000 |
| *Okwata* | 5 | 5 | 4 | 0.420 | 0.346 | -0.105 *NS* | 2.4 | 0.750 |
| *Otãngani* | 5 | 5 | 4 | 0.700 | 0.564 | -0.134 *NS* | 3.0 | 0.750 |
| *Premier Choix* | 5 | 5 | 4 | 0.600 | 0.528 | -0.026 *NS* | 3.0 | 0.750 |

*NS* Not significant, ** *P*-value < 0.01.

# 4. Reaping the fruits of trade

When he visited Lake Onangué in the 1960s, Sautter (1966) took note of the local manioc landraces grown in Nombedouma. In total, he inventoried 17 landraces, many of which were still grown when I conducted my surveys in 2006 (*e.g.*, '*Putu*', '*Ntse-Putu*', '*Oyogho*', '*Bakõngo*', '*Adyumbo*', '*Regholoto*', '*Evizo-Vizo*', '*Matadi*', '*Ikwãmba*'). However, I found also a large number of landraces that Sautter did not see, and recorded in total 46 landraces in Nombedouma while saturation curves suggest there may be actually more[50].



## 4.1. A positive attitude to diversity

In forty years, the Myènè have accumulated an impressive collection of manioc landraces, among the largest I found in Gabon, and some of the highest recorded in Africa at the village scale. Myènè farmers are collectors. They manifest a great interest in diversity, and regularly bring back a few cuttings from new varieties they discover while travelling. However, their search for diversity does not stop with already existing landraces. In Odimba and Nombedouma alike, farmers also extend their curiosity to self-sown manioc seedlings germinating in their farms. In Nombedouma, I recorded 14 landraces which farmers said were clones of manioc volunteers, and farmers in Odimba confirmed six other cases. Besides, some of these clones of seedlings were named after the villages where the volunteers were found, suggesting that the incorporation of manioc volunteers is not restricted to just Odimba and Nombedouma.

### 4.1.1. Seedlings in Africa

In South America, preparing cuttings from manioc volunteers is a common practice among Amerindian farmers (see for example the Aguaruna [Boster 1984b] and the Amuesha [Salick *et al.* 1997] in Peru, the Makushi in Guyana [Elias & McKey 2000, Elias *et al.* 2001a, McKey *et al.* 2001], the *caiçara* in Brazil [Sambatti *et al.* 2001], the Palikur and the Wayãpi in French Guiana [Pujol *et al.* 2005b, Duputié *et al.* 2009b]).

[50] For example, four landraces that Sautter recorded in 1966 ('*Ngwekyakya*', '*Efouma*', '*Akoulwe*', '*Bõmbe*') are missing from my listings, but I have no certainty that I would not have found them by interviewing more farmers in Nombedouma.

Incorporation of manioc seedlings by African farmers never appears to be but marginal (*e.g.*, Fresco 1986, de Waal *et al.* 1997, Manu-Aduening *et al.* 2005) or motivated by the necessity to obtain sound planting material in regions severely affected by the CMV pandemic[51], such as in East Africa (Jennings 1963, 1970, Kizito *et al.* 2005, 2007), where farmers used seedlings as a source of virus-free planting material (Lozano 1989) to rebuild their stocks of cuttings after severe CMV outbreaks.

### 4.1.2. Cognitive selection among the Myènè in Gabon

In Gabon, Myènè farmers look after manioc volunteers just like the Amerindians do. When they identify a volunteer with unusual features, they multiply it, and later give it a name. Until now, no one had described behaviours toward volunteer seedlings in Africa comparable to those observed among Amerindian farmers; the ways the Myènè exploit this diversity to 'breed' new landraces are exceptional for Africa, in many respects; firstly, by their non-purposive causality (Shigeta 1996). Unlike those African farmers who also use manioc volunteers, but from necessity rather than from a real understanding of the potential of manioc volunteers as a source of novelty, there is no practical usefulness behind the interest Myènè exhibit for manioc volunteers, beyond a genuine attachment to diversity. In Nombedouma, where I documented the highest number of (alleged) clones of seedlings, disease prevalence is low (see the distribution map of CMV strains in Gabon, in Legg *et al.* 2004). The farmers I interviewed were generally unconcerned by manioc diseases. Sourcing sound planting material thus did not appear to be a motive for Myènè farmers, not even in Odimba, despite the recent outbreak of anthracnose. Farmers fostered indiscriminately all volunteers in their farms and eventually harvested them all, although only the most unusual plants appear to be multiplied and given a name. Quality of the roots produced by manioc volunteers was also a minor concern to the Myènè, who prioritized the outer appearance as a criterion to retain a volunteer. Shigeta (1996) coined the term 'cognitive selection' to contrast this form of selection that favours diversity for its own sake, from more utilitarian approaches to diversity that value performance.



[51] The CMV is one of the major threats to African manioc. The Ugandan variant (EACMV-Ug), one of the most virulent recombinant strain of the virus, is now spreading westwards, and was reported in south-eastern Gabon in 2003 (Legg *et al.* 2004).

Secondly, unlike in most documented cases in Africa where the use of volunteers is not only less developed but also unevenly distributed among sites and even among farmers within a single village (Mkumbira *et al.* 2003, Kizito *et al.* 2005, 2007), the use of manioc volunteers among the Myènè is not an individual initiative (as in de Waal *et al.* 1997, Chiwona-Karltun *et al.* 1998, and Manu-Aduening *et al.* 2005), but a truly culturally anchored practice, acknowledged by all farmers, Galwa and Orungu alike. Remarkably also, only the Punu in Odimba discarded volunteers. Myènè farmers, in contrast, let them grow, or sometimes thinned out volunteers where they were too clumped.

## 4.2. Insights from historical hindsight



In other parts of Gabon, I recorded manioc seedling densities ranging from 0.7 to 9.3 volunteers $\times m^{-2}$. Earlier studies in Cameroon revealed that seedlings could indeed be found at very high densities in newly burned fields in African manioc settings (McKey *et al.* 2001). The necessary biological substrate for local breeding of varieties thus exists. However, in most studies conducted in Africa, manioc landraces always turn out to have originated elsewhere (see Chiwona-Karltun *et al.* 1998, Manu-Aduening *et al.* 2005, Delêtre 2004).

Manioc seedlings are the only available source of *de novo* diversity at the local scale (Cury 1993, Sambatti *et al.* 2001), but a pointed knowledge of the biology of manioc, and above all a genuine interest for the plant and for diversity, are required for farmers to start experimenting with manioc volunteers. Although fostering manioc volunteers is not in itself restricted to the Myènè in Gabon, the use of manioc self-sown seedlings to 'breed' new landraces is however strictly unique to the Myènè, and so far unprecedented in Africa. In what are the Myènè different?

Perhaps in the fact that, unlike the Tsogho[52] or the Fang[53] in Gabon, and unlike most populations in most of East and West Africa, who first snubbed manioc but gave in eventually to the coercive encouragements of the colonial administration (Jones 1959, Carter *et al.* 1992), the Myènè were the main actors of the onset of manioc farming on the coast of Gabon.

[52] See Chapter IV.

[53] See Chapter V.

### 4.2.1. The "São Tomean exchange"

Unlike in Congo or in São Tomé[54], there was no motive for the Portuguese to introduce manioc and maize in Gabon. Instead, the early appearance of these crops on the coast reinforces the idea that their adoption in Gabon was spontaneous, and probably triggered off by the Myènè themselves.

At the cross-roads of all major cultural influences—Portuguese, Brazilian, and Dutch at Cape Lopez, English and French in the estuary, Vili [B.503], Ghisir [B.41] and Eviya [B.301] at Adolinango, and Kèlè [B.22], Seke [B.21], and Punu [B.43] at Setté-Cama—the Myènè have been profoundly marked by their privileged geographic positions on the Ogooué and along the coast. In all aspects of their cultural and material life, down to their music (Lebomin & Bikoma 2005), they have developed a remarkable capacity to assimilate foreign elements. Several of the early observers of the populations in Gabon have indeed drawn attention to the Myènè's desire to copy the Europeans, as a way to demarcate themselves from other populations (**Ayogo**, "the advanced", as the Myènè singled themselves out from the **Anõngo**, "the primitive" of the interior; see Raponda-Walker 1960, Patterson 1975 and Merlet 1989). This desire showed in their clothing, housing, and in the way some of them adopted Portuguese, Dutch or English names (Patterson 1975, Merlet 1989). The Myènè language, likewise, was considerably enriched by regular contacts with Portuguese traders, and the Myènè borrowed several words not only from Portuguese, but also from English and French (Raponda-Walker 1933, Reynard 1955, 1956).

In Luanda, Jones (1959) similarly showed how willing the people from the kingdom of Kongo were to mimic the Portuguese, and how this facilitated the transmission of cultural elements from the Portuguese to the Africans. Manioc, which the Portuguese started to grow ca. 1560 near their trade forts, spread spontaneously among the neighbouring tribes, and diffused rapidly along the Congo River (Jones 1957, Carter *et al.* 1992). The same may be true of the Myènè in Gabon. Some of them accompanied Portuguese traders in their voyages to Brazil and to São Tomé (Raponda-Walker 1933, Patterson 1975). Manioc most certainly whetted the curiosity of the Myènè, who readily adopted it, perhaps as a way to distance themselves ever more from other tribes.

[54] In Congo and São Tomé, manioc was originally grown to provision ships bound for Brazil. The earliest written account of manioc cultivation on the African coast is that of Samuel Brun in 1612 in Congo (Jones 1959). The Portuguese probably introduced manioc in São Tomé shortly after (*ibid.*).

Several crops suggest the importance this "São Tomean exchange" may have played in facilitating the early diffusion of manioc farming among the Myènè. In the 1480s, the Portuguese embarked on developing their colony on the islands of São Tomé and Príncipe, and introduced sugarcane, calling for an important contingent of servile labour (Reynard 1955). Throughout the 16th century, Portuguese settlers populated the previously uninhabited island of São Tomé with thousands of slaves drained from Loango, Mayumba, and Cape Lopez (Reynard 1955). At the heyday of the sugar colony, in the mid-1500s, São Tomé numbered between 5,000 and 6,000 slaves (Patterson 1975). Sugarcane was probably transported to Gabon at a fairly early date. Van Linschoten (from Patterson 1975 and Gaulme 1981) mentions sugarcane among the Mpongwe [B.11a] around 1600. From the Portuguese, the Myènè had apparently also learned how to prepare wine (**mussungu**[55]) from the juice of the sugarcane (Gaulme 1981).

Maize is yet another crop that the Portuguese introduced to São Tomé. Its introduction coincided with the development of sugarcane plantations on the island, between 1520 and 1530. The Portuguese introduced maize originally to feed the slaves they brought from the continent (Miracle 1965, McCann 2001), but they were almost certainly also responsible for its introduction into Gabon.

Maize is known in Gabon under a variety of names. Among riverine tribes of the Ogooué and the Ngounié (Galwa [B.11c], Ghisir [B.41], Tsogho [B.31], Eviya [B.301] and Nzabi [B.52]), maize is however known as **putu** or **poto**, or words derived from the same linguistic root (**poti**, **potsi**, **mpotsu**, **mpotyè**; Raponda-Walker 1952). Because the forest made the cultivation of millet and sorghum impossible beyond Mayumba, people in the south-western part of Gabon had no local equivalent of maize, and unlike people from the Congo basin, who substituted to maize the names of their traditional cereals (**masa**, generally used for millet; see Bahuchet & Philipson 1998), they made up a name for this new crop from the only referential they had, *i.e.*, the people in contact to whom they discovered this new crop, the Portuguese, **putu** in Myènè [B.11], **m'putu** in languages from the Kikongo group [H.10]. It is possible that the Myènè borrowed the word from the Vili [H.12], who they displaced from Setté-Cama ca. 1600-1650 (see Gaulme 1981). However, maize cultivation beyond Mayumba is not attested by Battell in 1610, nor by Brun in 1611 (Bahuchet & Philipson 1998), supporting a direct transmission of maize from the Portuguese to the Myènè, rather than a mediation from the Vili [H.12].

[55] Or **muzungu**, "The White" or "The European", in several Bantu languages of RD Congo.

Manioc probably followed a similar route. Manioc was introduced fairly early to São Tomé, probably in the mid-16th -early 17th century (Jones 1959). Like maize (Juhé-Beaulaton 1990), it transited most likely first by the islands of the Bight of Benin before it was introduced on the continent. Since the 1650s, the islands had become a transit point for slave trade. The Portuguese had abandoned sugar production in São Tomé, and developed instead manioc farming to provision ships bound for Brazil or Cuba (Jones 1959). By 1700, manioc had become an important food crop on the island, and already in 1690, Barbot witnessed in São Tomé the preparation of manioc flour "in the Brazilian manner" (Jones 1959).

Manioc most likely arrived to the Myènè around 1700-1750, as trade exchanges intensified on the coast (Sautter 1966, Patterson 1975, Gaulme 1981). Because manioc digitated leaves reminded them of the kapok tree (*Ceiba pentandra* [L.] Gaertn., Malvaceae), the Myènè called the new crop **oguma**[56] (Raponda-Walker 1952). The linguistic comparison of Myènè and Kikongo words for manioc (**oguma** in Myènè, **mayaka** in Kikongo) supports, like in the case of maize, an independent introduction of manioc in Gabon. The Myènè apparently also learned from the São Tomeans the ways to detoxify manioc roots. While in most of Gabon **manioc bakõngo** is the main dish made from manioc, the Myènè have a unique way of grinding and cooking manioc in the form of roasted flour, virtually unknown in the rest of the country[57] (Jones 1959, Sautter 1966, Gaulme 1981, and personal observation).

Also known as **gari** or **attieke**, manioc flour is popular in West Africa, but it appears completely absent from Central Africa[58], where **chikwangue**[59], **fufu** and manioc *bâtons* are the most common ways to prepare manioc (Lancaster *et al.* 1982). The way the Myènè prepare manioc flour is very similar to that of Brazilian Amerindians, and the name they give to this preparation, **fariña**, is actually a word directly borrowed from the Portuguese (Reynard 1955). In the 19th century, Raponda-Walker (1960) mentions manioc flour as a common foodstuff that the Orungu [B.11b] transported in pirogues to the Gabon estuary to sell it to the Mpongwe [B.11a], suggesting the Orungu had known its preparation for some time already. In the estuary, conversely, manioc farming did not

[56] The vernacular name for the kapok tree, in Myènè.

[57] It is, in fact, also prepared by the Ghisir, but I expand on this later in Chapter IV.

[58] The technique of **gari** spread also along the coast of Cameroon, most likely from Nigeria.

[59] A kind of loaf prepared with the manioc dough (see Lancaster *et al.* 1982).

develop before ca. 1865 (Raponda-Walker 1952, Rossel 1987). Most likely, the presence of the French and the British in the Gabon estuary, more tangible in the 1840s after the slave trade was abolished (Walker & Reynard 1956, Merlet 1989, 1990a), weakened the influence of São Tomé and limited direct exchanges with the Portuguese.

Many other plants of New World origin have names in Myènè that show how much the proximity of São Tomé directly impinged on Myènè agriculture, and emphasize the role of the Portuguese in introducing new foods into Gabon (*e.g.*, maize[60], onions[61] [*Allium cepa* L., Alliaceae], mangoes[62] [*Mangifera indica* L., Anacardiaceae], potato[63], and pineapple[64] [*Ananas comosus* [L.] Merr., Bromeliaceae]).

### 4.2.2. 'Putu', manioc fetish of the Orungu



Similarly, many manioc landraces bear names which leave no doubt on their origin (*e.g.*, '*Putu*', '*Ntse-Putu*'[65], and '*Otãngani*'[66]). Among them, '*Putu*' deserves a particular attention. '*Putu*' is a very old landrace, and as its name suggests, cuttings of this landrace were probably among the first the Myènè received from the Portuguese (Raponda-Walker & Sillans 1961). Sautter (1966) and Gaulme (1981) also recorded '*Putu*' among the Mpongwe [B.11a], in Libreville, and the Nkomi [B.11e] in the Fernan-Vaz (Omboué).

In Odimba, farmers recounted that they used to plant '*Putu*' before any other plant. The landrace seems however to have lost much of its agronomic importance after original cuttings were replaced by other landraces distributed to farmers by the local council, but it has not lost its cultural significance. Those farmers who still grow '*Putu*' nevertheless still plant it first when beginning the plantation of a new farm.

Landraces such as '*Putu*', '*Ntse-Putu*', and '*Otãngani*', highlight how the strong ties between Myènè and Europeans, especially the Portuguese at São Tomé, played a major role not only in the diffusion but also in the 'cultural domestication' of manioc. Because the Myènè started to grow manioc on their own initiative, they probably developed a less

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[60] **putu** ("the Portuguese" , in Myènè).

[61] **cebola** in Myènè, *sabola* in Portuguese.

[62] **oba w'atãnga**, "the mango of the Whites", by opposition to the African mango (*Irvingia gabonensis* [Aubry-Lecomte ex O'Rorke] Baill., Irvingiaceae), known in Gabon as **odika**.

[63] **mõngo y'atãnga**, "the potato of the Whites".

[64] **ikoko ni atãnga**, "the sugar of the Whites".

[65] "Portugal" (*lit.*, "the land of the Portuguese", in Myènè).

[66] "The White" (*i.e.*, "the European").

ambivalent attitude towards manioc farming than did other populations in regions where manioc cultivation was made compulsory by authorities (as in the Ngounié and the Woleu-Ntem [67]), and where farmers developed an ambivalent attitude to the crop, considering manioc mainly as a mere food supply rather than as a plant worthy of more particular interest.

## 4.3. Manioc diversity in Myènè farms

By fostering manioc volunteers in their farms, and preparing cuttings from volunteer seedlings, either as new landraces or as new clones within an already existing landrace, Myènè farmers in Nombedouma maintain high levels of genetic diversity and possibly increase genotypic diversity in their farms and at the level of the entire village. Both average allelic richness and genotypic diversity were high in Nombedouma, even though my sample for that village was comparatively small. All five landraces analyzed were polyclonal.

Yet again, named diversity was not entirely matched by genetic diversity, and several names referred to the same multilocus genotype. Whether this is an effect of 1) a high rate of mislabelling, or 2) of a redundant naming system, is unclear. The size of the sample does not permit deciding between the two hypotheses, but since many of the apparent homonyms or mistaken names were all linked to the same farmer (OF), the former hypothesis seems the most plausible. It also suggests that this redundancy is not very important for understanding diversity patterns at the scale of the entire village.

Surprisingly, when contemplating the genetic diversity of manioc landraces in Odimba, field observations were not borne out by figures. Since using manioc volunteers for preparing new cuttings is an open practice among Myènè farmers, polyclonality should be found in most—if not all—landraces (see Elias *et al.* 2001a, Duputié *et al.* 2009b). Instead, I found most landraces in Odimba to be predominantly monoclonal (average clonal richness, $R = 0.082 \pm 0.078$).

Many landraces were sampled from only one farm (*e.g.*, '*Premier Choix*', '*Atolizo Izõmbi*', '*Epãndja*'), which increases considerably the chance that all five plants collected for a given landrace will be clonemates. However, even among those landraces which were sampled from more than one farm, many were strictly monoclonal ('*Bakõngo*', '*Ipãndo Jaune*', '*Côte d'Ivoire*'), or nearly so ('*Matadi*', '*Lãndi-Lãndi*', '*Madouedoue*').

[67] See next chapters.

What is more, polyclonal landraces were polyclonal at the village level, but not at the level of the farm. In fact, farmers grew the same set of *named* landraces (*e.g.*, '*Bakõngo*' W, '*Ntselele*', '*Ngwesuku*'), but each of them grew a different set of *clones*. In fact, 16 (61.5%) of the 26 MLGs identified in Odimba were grown by only one farmer.

In the other villages I surveyed, even in those where farmers discarded manioc volunteers and showed little interest in diversity (as among the Fang in northern Gabon[68]), farmers shared a common pool of clones. When, for a given landrace, several clones existed in the village, polyclonality existed also at the level of the single farm, not just at the level of the village, as in Odimba.

The clearly non-random pattern of distribution of diversity among farmers in Odimba is most likely an artefact of the recent aspiration of local councils to promote farming in the region, and develop the local economy by increasing the insertion of villages into a market system supplying Port-Gentil. The project, however, required that large areas be planted with manioc, while the concurrent outbreak in Odimba of anthracnose had resulted in a dearth of planting material. The Izunu association, in charge of the project, alleviated this shortage by supplying farmers with large bundles of cuttings imported mostly from Lake Avanga (A.M. Aperano[69], pers. comm.), where the association had developed several pilot farms.

The clear patterns of distribution of genotypic diversity among farmers suggest that imported cuttings were dispatched on a case-by-case basis, each farmer receiving a different assortment of cuttings. Besides, many cuttings were given to farmers without mentioning the name of the landrace, resulting in a large number of 'unknown' manioc plants (not included in the analyses) in Odimba. This massive introduction of planting material, still recent at the time I made my surveys[70], appears to have made a clean sweep of any possible pre-existing pattern of diversity, and diluted the contribution of manioc volunteers to the general diversity in the village.



[68] See Chapter V.

[69] Coordinator of the Centre Izunu (Centre Agro-Alimentaire de Production, de Vulgarisation et de Formation en Entreprenariat Agricole) for the Conseil Départemental de Bendje, in Port-Gentil.

[70] Cuttings were distributed to farmers only two or three years before I visited Odimba.

### 4.3.1. The importance of local seed systems

Local farming systems are generally self-sufficient when it comes to sources of germplasm for planting. The resilience of traditional farming systems has been emphasized in several studies, on beans (Haugen 2001), ensete (Shigeta 1990, 1996), potato (Johns & Keen 1986, Thiele 1999), yam (Scarcelli *et al.* 2006), and manioc (Boster 1986, Salick *et al.* 1997, Peroni & Hanazaki 2002, Emperaire & Peroni 2007, Pujol *et al.* 2007). Farmers are managing large and diversified collections of landraces, gathering new cuttings through their own exchange networks (the social component of resilience of local farming systems, see Berkes & Folke 1998), but they also amplify diversity by repeatedly re-injecting alleles through the incorporation of manioc volunteers, either by assimilating them to pre-existing landraces, or by multiplying and naming remarkable individual plants (Elias *et al.* 2001a, McKey *et al.* 2001). This double "buffer effect" (Peroni & Hanazaki 2002) is however endangered by the contrasted saturating effect of mass distributions of planting material, especially when these occur within a short timescale or within a restricted geographical area.

### 4.3.2. Cultural and genetic erosion

Instead of targeting villages in need and providing them with an adapted answer, direct seed distributions, when undertaken without prior knowledge or inadequate diagnosis of informal 'seed'[71] systems (in particular, ignoring the crucial role of manioc soil seed banks, which confer the farming systems a capacity to tackle catastrophic crop failures without necessitating an external supply of germplasm; see Pujol *et al.* 2007), may inundate farmers with large numbers of propagules and may be, in some instances, detrimental to local diversity (Almekinders *et al.* 1994, Sperling & Longley 2002). The risk is that direct 'seed' distributions will eventually lead to a homogenization of diversity at the regional scale, and tone down the particularities of manioc farming among different populations. In Odimba, the clearly non-random patterns of diversity at the village scale suggest that the distribution of exogenous stem cuttings orchestrated by the local council provoked a complete 'seed' replacement in the village, and resulted in the near loss of very old landraces (*e.g.*, '*Putu*').

[71] 'Seed' is to be here understood with the meaning of propagule, regardless of the nature of the material used for propagating landraces (seed, tuber or stem cutting).

### 4.3.3. Cultural flexibility and cultural resilience

Beyond their obvious deleterious effects on the cultural and patrimonial value of diversity, bulk distribution, by creating a dependence on external sources to supply diversity (de Barbentane 2001), also endangers the resource resilience of local farming system. Emperaire *et al.* (1998) have highlighted the fact that the loss of folk biological knowledge can indeed be more harmful to diversity than the loss of the landraces themselves.

History has shown that the Myènè are culturally flexible, their 'traditions' having been enriched by a continual assimilation of foreign elements. The Myènè absorbed the new, but they did not drop the old. They added the new crops they discovered in contact with the Portuguese to their own crop portfolio, without however dismissing their indigenous crops. The same holds true of manioc landraces, of which farmers in Odimba and Nombedouma have amassed large collections. This singular cultural resilience (*sensu* Begossi 1998) may contribute to preserving their outstanding ways to exploit an untamed—and, outside the Myènè realm, largely untapped—but crucial source of diversity.

**Synthesis**

The Myènè are the first documented case in Africa of a truly autochtogenous[72] dynamic of *de novo* creation of manioc landraces. However, by increasing the risk of creating dependence on outside sources of diversity, the meddling of local authorities in the seed system of the Myènè may endanger the continuation of the cultural processes that make the Myènè a unique example of manioc farming in Africa. Their singularity stems essentially from their strategic position in pre-colonial trade networks. The positive response of Myènè populations to the Portuguese presence at São Tomé sharpened their curiosity for new crops as for other elements of the São Tomean culture. Among the Myènè, manioc found, literally and figuratively, a favourable substrate to take root in Gabon.

[72] That is, in the present case, landraces that were created locally (see definition in Chapter I).



**Plate III**

Preparation of cuttings (**erere z'ilôti**) before planting (a). Three to five cuttings are buried together horizontally (b) and covered with soil.

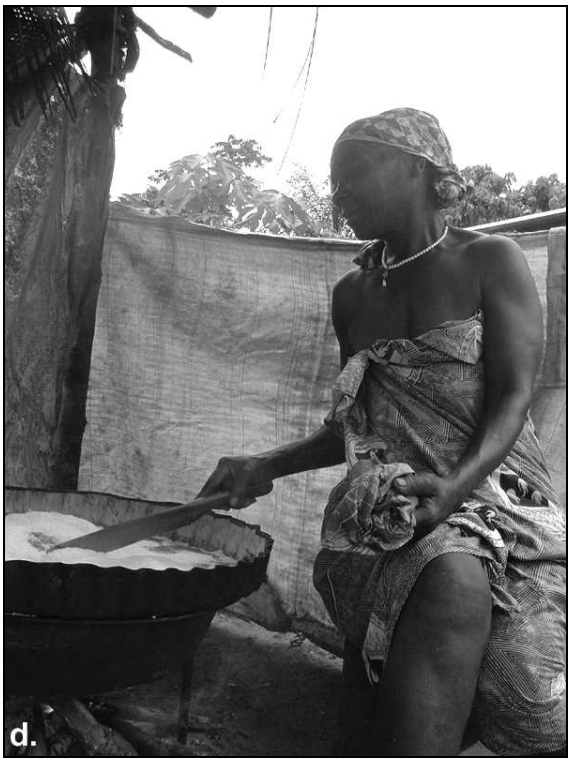




**Plate III** (continued)

Preparation of **fariña**. Fresh roots are grated, sundried, and then sifted (c) and roasted (d) on a cooking plate (**õmbumbu**). This preparation in "the Brazilian manner" is most likely a direct transfer of technique from the Portuguese established in São Tomé to the Myènè with whom they were in close trade partnership.

# Chapter IV

## *"What is food to one, is to others bitter poison"*

**Lucretius** (96 BC - 55 BC)



### Douani

01°02'41.4"S, 010°40'59.5"E

*Tsogho (B.31)*

### Mandilou

01°17'17.2"S, 010°36'47.3"E

*Ghisir (B.41)*

# Abstract

Ease and speed of manioc diffusion and adoption in the different regions of Africa was largely influenced by indigenous agriculture prior to the arrival of the crop. Whether populations were mostly growing yams, plantains, or cereals, considerably impinged on manioc substitutability, and either facilitated or slowed down its insertion into the local crop portfolio.

In West Africa, maize, sweet potato and manioc were all introduced in the 16th century from the Americas (Jones 1957), but while maize and sweet potato were readily adopted by West Africans, manioc, conversely, stagnated on the coast and did not spread inland until late in the 18th century. Sweet potato could easily be substituted for plantain or cocoyam (*Colocasia esculenta* [L.] Schott, Araceae), while maize was similar enough to sorghum (*Sorghum bicolor* L., Poaceae) and millet (*Eleusine coracana* L., Poaceae) to find a place in farmers' portfolio of crops. In contrast, West Africans did not 'tame' manioc until the late 18th century. Jones (1957) hypothesized that manioc bitterness was the main curb to manioc adoption in West Africa, where the Portuguese presence was more discrete than in Congo. The return of African slaves from Brazil (the "Brasilias", see Verger 1968), who contributed to the diffusion of efficient techniques to detoxify manioc, greatly hastened manioc adoption by the populations of the interior after 1750 (Jones 1957).

In all southern Gabon, plantains were the main staple long before the arrival of manioc (Raponda-Walker 1960). Plantains do no require particular processing. The contrasting complexity of manioc detoxification processes, and the planning they involve, were probably curbs on manioc adoption, and the crop seems to have only grown in importance as a result of the drastic socioeconomic and demographic changes suffered by the local populations in the early 20th century.

Through the comparison of Tsogho's [B.31] and Ghisir's [B.41] involvement in pre-colonial trade and participation to the "okoumé fever" that characterized Gabon in the 1910-1920s, I investigated in this fourth chapter the modes of cultural transmission of manioc "technology" and their effects on the evolution of farmers' preferences for bitter or sweet manioc and behaviours towards manioc volunteers.

# 1. The "king" okoumé: Mitsogho and Ghisir ca. 1900

The Tsogho[73] [B.31] (Guthrie 1948, Maho 2003) live in the du Chaillu massif, in central Gabon (Upper Ngounié) and number ca. 25,000 (Lewis 2009). Their territory stretches from Sindara, in the North, to Lébamba in the South (Map 4.1), across a mountainous region long inaccessible to European traders and explorers (see Raponda-Walker 1960). Facing the Tsogho, on the opposite banks of the Ngounié river, the Ghisir[74] [B.41] territory spreads beyond Fougamou, over large extents of savannah grasslands which gradually replace the forest as one travels south towards Mouila.

## 1.1. Origins of the Tsogho and the Ghisir

### 1.1.1. The Tsogho

According to oral tradition, the Tsogho left the Ivindo region in the late 16th century, to escape from the incessant harassment of the Kèlè[75] [B.22] who raided their villages (Raponda-Walker 1960, Gray 2002). The Tsogho followed the Ofooué valley to the west, further down the forest, until they reached the Ikoï basin and finally settled on the right bank of the Ngounié River, in the Du Chaillu massif (see Appendix A2).

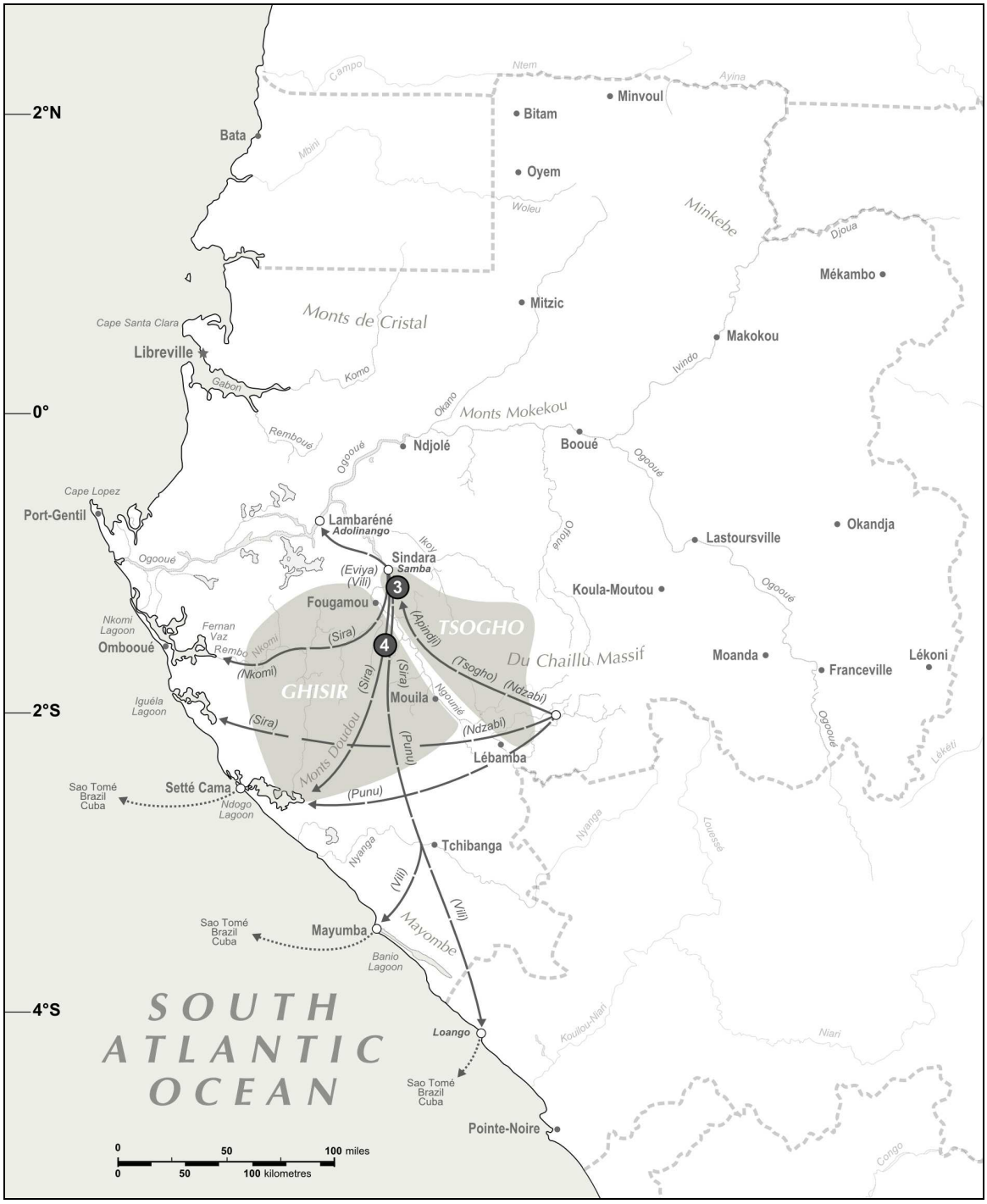
In the shelter of the mountains, the Tsogho remained, until very late in the 19th century, relatively spared from the struggles over access to trade that tore apart their Ghisir neighbours (Raponda-Walker 1960, Gray 2002). They first encountered Europeans when the French explorer, Paul du Chaillu, visited their villages in 1865 (Merlet 1991). No one before him ever managed to travel that far in the hinterland. All previous attempts had failed (Bodwich, in 1815, and du Chaillu himself, in 1857), and expeditions had bumped into the hostility of riverine tribes, who feared that Europeans would imperil their dominion over trade (see Merlet 1991). Until late in the 19th century, the Ngounié was left practically untouched by European influence. Ca. 1890, trade factories were established at Sindara, near the Samba falls, followed by catholic missionaries who founded "Notre-Dame des Trois Épis" (Raponda-Walker 1960). The next year, the administrative post of Sindara was created, marking the start of the colonial era in southern Gabon.



[73] Tsogho or Mitsogho, and sometimes also found as Kangè (Raponda-Walker 1960).

[74] Also called Sira, Eshira, and Ashira (see table in Appendix A1).

[75] Sometimes confused with the Ngom [B.22b].




**Map 4.1. Present distribution of Tsogho and Ghisir in Gabon**. Throughout the 19th century, the Samba falls on the Ngounié river, near Sindara, were a key point for commerce, and a junction of several trade routes (arrows), linking the interior of Gabon (Tsogho [B.31], Ndzabi [B.52], Sangu [B.42]) to the Ogooué (Galwa [B.11c], Enenga [B.11f]). Based on Maho (2003) and Merlet (1991). The location of Douani ❸ and Mandilou ❹ is reported on the map.

### 1.1.2. The Ghisir

The Ghisir are related to the Myènè, and were long thought to be a sister group of the Galwa and the Orungu (Raponda-Walker 1960). Recent studies support however a "southern" origin, suggesting that the Ghisir may have first migrated together with the Vili [H.12] from the region of Bas-Congo to the present Ngounié (Van der Veen 2001), ca. 1600, and possibly as far as the middle Ogooué in contact with the Myènè, until they were driven back by the Galwa [B.11c] in the course of the 18th century (Raponda-Walker 1960).

Unlike the Tsogho, the Ghisir experienced directly the consequences of European presence in southern Gabon. By the end of the 19th century, the attraction of European merchandises had gradually upset the social cohesion of Ghisir communities (Raponda-Walker 1960, Merlet 1991). Jealousy and fear had scattered their villages in a multitude of small hamlets, and when du Chaillu wandered again in the Ghisir plains in 1864, he noted that since his previous visit, six years earlier, several elements of the Ghisir material culture had vanished in favour of imported items from Europe, which the Ghisir had obtained through trade with the Myènè (Raponda-Walker 1960, Gray 2002).

## 1.2. The changes: 1890-1930

In the years following the installation of concessionary companies at Sindara, populations in southern Gabon experienced radical economic and social changes. Starting ca. 1910, the fast-growing exploitation of okoumé tolled the knell of conventional trade and contributed to the opening up the Tsogho realm, blurring territorial divisions between tribes (Gray 2002). In just about a decade, the "okoumé fever" spread among populations, attracting thousands of opportunistic wood-cutters from various ethnic origins. Farmers became loggers, and okoumé exports rose from 5,000 tons in 1902 to 135,000 tons in 1913 (Bouet 1980). Between 1916 and 1920, the unrestrained boom of timber industry provoked repeated food shortages, as the appeal of wage-labour turned young men away from their farming duties and labour force lacked in the villages for clearing new farms (Gray & Ngolet 1999).

Meanwhile, the "king okoumé", to reign on Gabon until it was overthrown by petrol in the 1960s, drained at Sindara thousands of people. Following the Fang [A.75], the Kèlè [B.22], the Ghisir, the Eviya [B.301], and the Punu [B.43], the Tsogho established their first villages at Samba at the turn of the century (Gray 2002).

## 1.3. Douani and Mandilou

### 1.3.1. The history of Douani

Douani (01°02'41.4"S, 010°40'59.5"E) is located on the Ngounié River, only a few kilometres away from Sindara and from the Samba falls. Vili[76] [B.503] in 1899 (Raponda-Walker 1960), Douani is now a small Tsogho community of about 20 families.

Long before the arrival of factories on the Ngounié, the Samba falls were an active commercial hub. Vili and Eviya held jealously that key position in the "relay trade" (*sensu* Chamberlin 1977) and controlled commerce with the Ogooué. Tsogho, Sangu [B.42] and Nzabi [B.52] sold them ivory, redwood, and slaves, which the Vili exchanged for manufactured goods with the Galwa [B.11c] and the Enenga [B.11f] (Gaulme 1981). In 1866, Bruce Walker reached the Samba falls and established there the first factory, followed by several others in the 1890s, in an attempt to bypass intermediaries and gain direct access to merchandises.

When the mission "Notre-Dame des Trois Épis" was founded at Sindara in 1899, Douani was an important Vili community (Raponda-Walker 1960), but smallpox epidemics broke out in 1898 and decimated most of their villages in the following years (Gray 2002), leaving way for other tribes to take their place. With the explosion of the timber industry a decade later, Tsogho replaced the Vili in Douani. Tsogho migration was later encouraged by the administration, and even in the late 1960s, many Tsogho villages were resettled outside the Du Chaillu mountains along roads and in the vicinity of Sindara (Gollnhofer *et al.* 1975).

### 1.3.2. The history of Mandilou

Located on the opposite side of the Ngounié River, along the RN3 in the outskirts of Fougamou, Mandilou (01°17'17.2"S, 010°36'47.3"E) is a large Ghisir community, formed of the grouping of two villages, Mandilou I and II. Mandilou II, where I stayed, is itself subdivided in nine districts, totalling 55 households.

Until 1928, Fougamou was no more than a repository for merchandises coming from Mouila and transiting towards Sindara (Raponda-Walker 1960). With the second boom of timber industry in the 1920s, the region became increasingly depopulated as thousands of

[76] The name of the river, Ngounié, comes from a Vili word, *nguni*. It is unclear, however, whether these are the Vili [H.12] related to the Kongo group, or a Vili subgroup related to the Nzabi. Linguistically, the Vili from the Ngounié are closer to the Ndzabi [B.52], and Maho (2003) classified them in the B group [B.503].

Ghisir joined the okoumé saga and moved to Lambaréné (Sautter 1966, Gray & Ngolet 1999). The recruitment of workers for the construction of the Fougamou-Sindara road, achieved in 1927, resulted however in a large Ghisir settlements around Fougamou, which the administration endeavoured to stabilize (*ibid.*). After 1928, the importance of Samba declined, and colonial power was transferred from Sindara to Fougamou.

### 1.3.3. Surveys

I visited Douani in October 2007. Fifteen farmers participated in the surveys. The majority (75%) of farmers I interviewed were Tsogho [B.31], two farmers were Eviya [B.301], and two were Ghisir [B.41]. I visited Mandilou in November and interviewed 18 farmers, all of whom were Ghisir.

I chose to consider mainly Douani, for which, owing to the more accessible size of the village, I have a more comprehensive dataset than for Mandilou. I will however parallel the two villages while discussing the consequences of the rapid changes of regional economy for agriculture in southern Gabon, and present the data from Mandilou in a complementary study, appended at the end of this chapter.

# 2. Agriculture among the Tsogho

## 2.1. The late onset of manioc farming

In his accounts of his first travel to the Upper Ngounié, in 1858, du Chaillu (see Merlet 1991) made only anecdotal mentions of manioc among the Ghisir and among the Apindji [B.303]. In contrast, peanuts (**pinda**, which du Chaillu confused with pistachios[77]) seemed to be the dominant crop in the region. When he finally reached the Tsogho in 1865, du Chaillu was impressed by the size of their peanut farms (see Merlet 1991 and Gray 2002), but still did not make any note about manioc, while he mentioned yams, bananas and sugar canes. When Raponda-Walker visited the Ngounié in 1899, manioc had made only timid apparitions among riverine tribes (Fang [A.75], Kèlè [B.22], Vili [B.503]), and was seldom found in the villages of the interior (Raponda-Walker 1952). Later, and particularly with the recurrent problem of provisioning workers on lumber camps (see Bouet 1977 and François 1991), the administration attempted to foster the adoption of manioc (Raponda-Walker 1952), but local populations persisted for a long time in growing bananas in preference to manioc.

## 2.2. The Tsogho farming system

Seasons are not as marked in the Upper Ngounié as they are in other parts of Gabon. Farmers in Douani only distinguish a long rainy season, which starts in November, and finishes in April, and a comparatively short dry season, starting in June and finishing in October. Farmers hence open new farms only once a year (Figure 4.1).

### 2.2.1. Agricultural calendar

In June, farmers start clearing new parcels, by first removing small shrubs, leaving the trees until July-August. Parcels are burned at the beginning of September, just before the first rains. Because farming is limited by seasonality, each farmer opens generally three farms every year, one for plantains, one for manioc, and one for peanuts.

[77] See also Pinkerton *et al.* (1804).

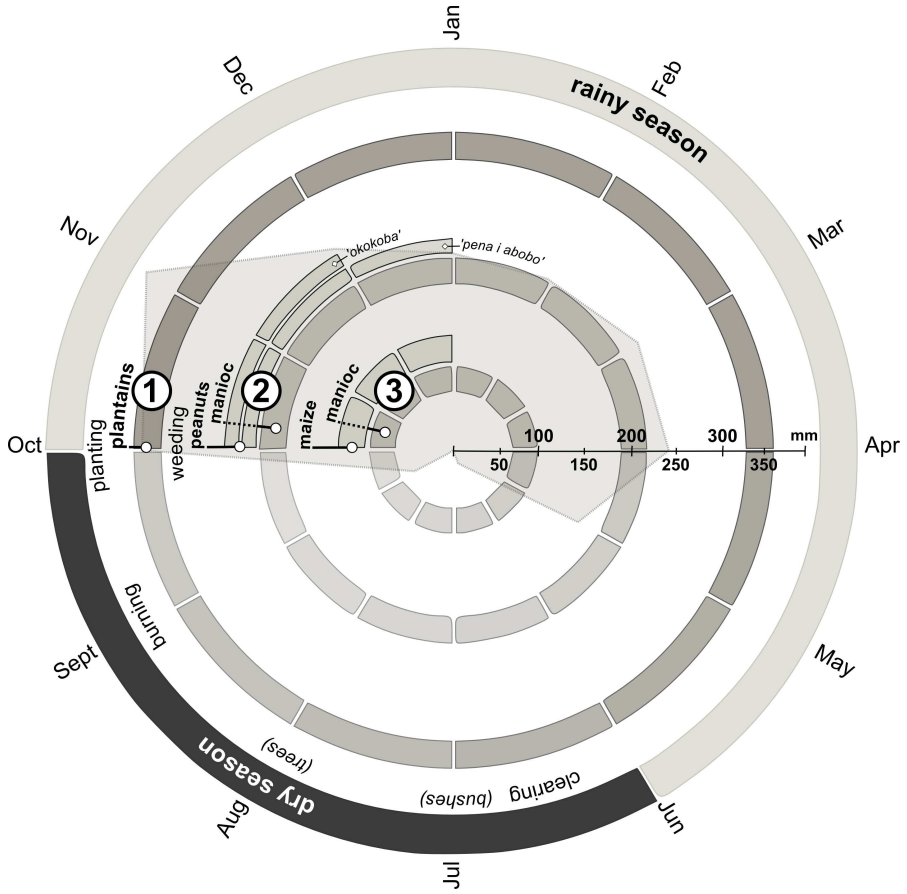



**Figure 4.1. The Tsogho agricultural calendar**. The Tsogho farming system is constrained by rainfalls (radar diagram), which allow farmers to open new farms only once a year. Plantains (1) and manioc (2,3) are their main staples, although the latter can be intercropped with maize or peanuts. In Douani, farmers grow two varieties of peanuts, '*okokoba*' and '*pena i abobo*' (2). The former matures in two months instead of three, and can be harvested as soon as December.



### 2.2.2. Composition of Tsogho farms

Tsogho farmers maintain many different landraces of manioc, taros, yams, and bananas, along with many different vegetables and greens (Table 4.1). Farmers distinguish **tságha** farms (①,③) and **tsete** farms (②). **Tsete** farms are reserved for peanuts. The Tsogho open **tsete** farms on short fallows (**poto**, fallow < 5 years), where trees have not grown too big, which considerably helps farmers with clearing. Peanuts are intercropped later with manioc, maize, and taros. **Tságha** farms are opened on primary or secondary forest (**píndi**, fallows > 10-15 years). They can be planted with plantains (**tságha kõndo**, ①) or manioc (**tságha mibegu**, ②).

**Table 4.1. Composition of Tsogho farms in Douani**.

| Crop | Latin name | Vernacular name | | | Varieties |
|---|---|---|---|---|---|
| | | ***Tsogho*** *(B.31)* | ***Eviya*** *(B.301)* | ***Eshira*** *(B.41)* | |
| Aubergines | *Solanum* spp. | **Pibi, Pivi** | **Tsaghale** | **Mbala** | |
| Bananas | *Musa acuminata** | | | **Ditoto di banana Ditoto di tsokodo** | '*Petits doigts*' |
| Folon | *Amaranthus* spp. | | | **Mignãmbi** | |
| Gombo | *Abelmoschus esculentus* | **Mibôdô** | **Mibôdô** | **Dõngo Dõngo** | |
| Maize | *Zea mays* | **Poto** | **Poto** | **Putu** | |
| Manioc | *Manihot esculenta* | **Eghõngo** | | **Ghigõngo** | |
| Peanuts | *Arachis hypogaea* | **Pèna** | | **Pínda** | '*Okokoba*' '*Pena ia bobo*' |
| Peppers | *Capsicum* spp. | **Ndõngo** | **Nõngo** | **Nungu** | |
| Pineapples | *Ananas comosus* | **Iãnga, Reiãnga** | | **Difubu** | |
| Plantains | *Musa sapientum* var. *paradisiaca*** | **Kõndo** | **Nikõndo** | **Mipal** | '*Ditoto di tsokodo*' |
| Pumpkins | *Cucurbita maxima* | | | **Dilènge** | |
| Sorrel | *Hibiscus sabdariffa* | **Boko** | **Bokolo** | **Bukulu** | |
| Sugarcanes | *Saccharum officinarum* | **Mokoko, Mikoko** | | **Mussungu** | |
| Sweet potatoes | *Ipomoea batatas* | **Mõngo, Mabweta** | | **Eweta** | '*Aghega*' '*Jaune*' '*Efuga*' |
| Taros | *Colocasia esculenta* | **Kida** | **Kira, Dikõmbissa** | **Dilãnga** | '*Dilãnga ditsõndolo*' |
| Yams | *Dioscorea* spp. | **Mba** | **Mba** | **Mbala** | '*Bikubebe*' '*Mbalefuga murãmbi*' '*Mongõngõ*' |

* AA group; ** ABB group.

## 2.3. Manioc

There are only few market opportunities in Douani, and manioc is grown mainly for subsistence. Farmers may occasionally sell baskets of manioc *bâtons*[78] (2,000 FCFA for one bundle), bananas offshoots (5,000 FCFA for ca. 25 shoots) or palm wine (**tutu**) in the neighbouring town of Sindara, but the main income is provided by timber industry, which employs most of the men in the village.

### 2.3.1. Productivity

Tsogho farmers harvest manioc every so often, only to satisfy household daily needs. Farmers practice a type of harvest called 'piecemeal harvest'. They only unearth mature roots, leaving the rest of the plant intact. Harvest can thus be spread over 2-3 years. A farm is abandoned only when weeds have invaded the parcel, but may still occasionally provide farmers with fresh stems, from which they will prepare cuttings for the next growing season.

Yield was estimated from two landraces, '*Ndungu*' and '*Mutõmbi*', both of which were categorized by farmers as "bitter"[79]. '*Ndungu*' yielded ca. 5 kg of fresh roots per stalk[80], and '*Mutõmbi*' 3kg per stalk, although the root system was incomplete in the latter case.

### 2.3.2. Planting pattern

Tsogho farmers plant manioc stem cuttings (**pende**) in triads, respecting the natural orientation of the stem. Cuttings measure 30 to 35 cm in length, for ca. 1.5-2 cm in diameter. Stem cuttings are planted diagonally, with only about 10 cm sticking out. Two cuttings are planted parallel to each other, opposing a third one which is planted in the middle. Such disposition favours the development of roots at the basal extremity of the stem cutting, without interfering with the two other cuttings and leaving space for tubers to develop.



[78] The Tsogho manioc processing techniques are described in Appendix B6.

[79] No data are available for other landraces, as sweet manioc, contrary to bitter manioc, rots quickly if left too long in the soil once roots are mature. By the time I started my surveys, sweet maniocs from the previous season had already been harvested.

[80] 5.6 ± 1.7 kg, based on five measurements.

## 2.4. Embedded varietal diversity

Farmers in Douani listed more than thirty names of landraces, but recognized many of those to be synonyms. Twenty-seven names corresponded to "sweet" landraces (**mibegu mia niege**), while only six were categorized by farmers as "bitter" (**mibegu miã'ndoy**). Eight landraces were named after the yellow colour of their roots, in contrast with the vast majority of landraces found in Gabon which produce white roots.

### 2.4.1. Distribution of named diversity in Douani

Each farmer in Douani grew on average seven landraces, and a majority of sweet manioc (Table 4.2). 93% of farmers grew '*Motõmbi*' as their sole or principal bitter landrace. Other bitter landraces only accounted for a few cuttings in their owners' farms. Collections were balanced in size ($E_f = 0.96$), but farmers grew very disparate sets of landraces ($E_v = 0.66$).

Among the sweet landraces, yellow varieties were very popular. All confounded, yellow cultivars ('*Dikilikoko Di Chinois*', '*Dikilikoko Di Jaune*', '*Dame Jaune*', '*Eake A Tchozo*') were cited by 80% of farmers, just before '*Etadi*' and '*Mounzoumba*' (both 73%), '*Mana*' (67%), and '*Kwata*' (60%). '*Maboundinieghe*' was grown by half the farmers I interviewed, but was considered by some to be a synonym of '*Simbu*'. Farmers grew either one or the other, but the two names were never found together in the same farm. Confounded, '*Simbu*' and '*Maboundinieghe*' were grown by 73% of farmers.

### 2.4.2. Origin of landraces

Landraces are usually transmitted vertically, from the mother to her daughters, but many landraces I recorded (*e.g.*, '*Mbikini*', '*Otchaka*', '*Ciam*'[81], '*Moabi*') had also been acquired recently, during travels to Lambaréné and Libreville, or during visits to relatives.



[81] *Ciam* is in fact an acronym, standing for the "Centre d'Introduction, d'Adaptation et de Multiplication du Matériel Végétal" (CIAM). The CIAM is responsible, in Gabon, for the maintenance and diffusion of cultivars developed by IITA.

**Table 4.2. Distribution of named manioc landraces** (rows) **among farmers** (columns) **in Douani**. 'x' indicates where the landraces were found. R, B and W stand respectively for "red", "black" and "white", in accordance with the colour distinction made by farmers between the different morphotypes of '*Iake A Tchosso*' and '*Motombi*'. NS stands for "not specified", since not all farmers grew the different morphotypes, nor necessarily made the distinction.

| **Landraces** | | | **MAF** | **NJ** | **BBH** | **LMF** | **KA$_1$** | **MC** | **DV** | **BI** | **DL** | **PJ** | **KA$_2$** | **MM** | **BL** | **KMF** | **OC** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bate Bakõngo* [a] | | Bitter | | | | | x | | | | | | | | | | |
| syn. *Congo* § | | Bitter | | | | | | x | | | | x | | | | | |
| *Bokungu Boduli* | | Bitter | | | | x | | | | | | | | | | | |
| *Chinois* [b] | | Sweet | | | | | | | | x | | x | x | | | | |
| syn. *Dikilikoko Di Chinois* | | Sweet | x | | | | | | | | x | | | | | x | x |
| syn. *Jaune Chinois* | | Sweet | | | | | | x | | | | | | x | | | |
| syn. *Jaune* | | Sweet | | | x | | | | x | | | | | | | | |
| syn. *Iake A Tchosso Chinois* | | Sweet | | | | | | | | | | | | | x | | |
| *Dikilikoko Di Jaune* [c] | | Sweet | x | | x | | | | | | | | | | | | |
| syn. *Iake A Tchosso* | NS | Sweet | | | | | x | | | | | | | | | | |
| | R | Sweet | | | | | | | | | | | x | | | | |
| syn. *Eakea A Tchozo* | | Sweet | | x | | | | | | | | | | | | | |
| *Edám* | | Sweet | | | x | | | | | | | | | | | | |
| *Edodo* | | Sweet | | | | | | | | | | | x | x | | | |
| *Etadi* § | | Sweet | | x | x | | x | x | x | x | x | | x | x | x | x | |
| *Ibola* | | Sweet | | | | | x | | | | | | | | | | |
| *Kwata* § | | Sweet | x | x | | | | x | x | | x | x | | x | x | | x |
| *Maboundi* | | Sweet | | | | | | | | | | | x | x | | | |
| *Maboundinieghe* [d] | | Sweet | | | | | | | | x | x | x | x | x | | x | x |
| *Mana* | | Sweet | | | | x | x | x | x | x | | x | x | x | x | | x |
| *Mbikini* | | Bitter | | | | | | | | | x | | | | | | |
| *Moabi* [e],† | | Sweet | x | | | | | | | | x | x | | | | | |
| *Modiõmbe* [f] | | Sweet | | x | | | | | | | | | | | | | |

[a] '*Bate Bakõngo*' may be a synonym of '*Congo*'; [b] '*Chinois*' is most likely synonym of '*Jaune*', '*Dame Jaune*', '*Jaune Chinois*', and '*Dikilikoko Di Chinois*'; [c] '*Dikilikoko Di Jaune*' is synonym of '*Eake A Tchozo*' (in Eshira and Eviya[82]) and '*Iake A Tchosso*' (in Tsogho); [d] '*Maboundinieghe*' is probably synonym of '*Simbu*'; [e] '*Moabi*' is sometimes also called '*Oabe*' §; [f] '*Modiõmbe*' is most likely a deformation of '*Moundjõmba*', a probable synonym of '*Mounzoumba*' and, according to some farmers, of '*Kwata*', which is sometimes confounded with '*Kwata Mayumba*'.§ Previously recorded by Van der Veen and Bodinga-bwa-Bodinga (2002) among the Eviya. † Recorded by Raponda-Walker and Sillans (1961).

[82] In Eviya [B.301], **eake** means "manioc variety" (Van der Veen & Bodinga-bwa-Bodinga 2002).

**Table 4.2.** (continued)

| **Landraces** | | | **MAF** | **NJ** | **BBH** | **LMF** | **$KA_1$** | **MC** | **DV** | **BI** | **DL** | **PJ** | **$KA_2$** | **MM** | **BL** | **KMF** | **OC** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Motõmbi* [g] | NS | Bitter | | x | x | | | | x | x | | x | x | x | | x | |
| | W | Bitter | | | | | | x | | | | | | | | | x |
| | S | Bitter | | | | | | x | | | | | | | | | x |
| syn. *Mutõmbi* | | Sweet | x | | | x | | | | | x | | | | | x | x |
| *Mounzoumba* [j] | | Sweet | | | x | x | | x | x | x | x | x | x | x | | x | x |
| *Ndungu* | | Bitter | x | | | | | | | | | | | | | | |
| *Ngoneyem* | | Sweet | | x | x | | | | x | | x | | | | | | |
| *Ngoya* | | Sweet | | | x | | | | | | x | | | | | | |
| *Otchaka* | | Sweet | | x | x | | | | x | | x | | | | | | |
| *Pauline* | | Sweet | x | | | | | | | | | | | | | | |
| *Ciam* | | Sweet | | x | | | | | | | | | | | | | |
| *Simbu* | | Sweet | x | x | | x | | | x | | | | | | | | |
| *Yakotojo* [i] | | Sweet | | | x | | | | | | | | | | | | |

[g] '*Motõmbi*' is the Tsogho name for '*Mutõmbi*' (in Eshira); [h] '*Ndungu*' is also called '*Timbendule*'; [i] '*Yakotojo*' is probably a synonym of ' *Eake A Tchozo*'. [i] Possibly the '*Monãnzabe*' mentioned by the Myènè Orungu [B.11b] in Odimba.

## 2.5. Manioc volunteers

Farmers in Douani called **midènga**[83] every crop plant that grew spontaneously in their farms, including manioc volunteers. Farmers said that they systematically pull out manioc seedlings, but spare taro and yam volunteers. In all peanut farms, including those of the previous cropping season (September 2006) which had been since converted to manioc plantations, farmers had spotted manioc seedlings. All farmers were aware manioc volunteers originated from the seeds (**mibiè mia gõngo**[84]) produced by the plant in the previous farming season, and no farmer could recognize the landrace volunteers belong to.

### 2.5.1. Densities of volunteers

Seedling densities were estimated in 13 peanut farms, all of which had been cleared in September 2007. When I started my surveys, farmers had already started planting manioc in their **tsete** farms. Most fields had already been weeded once, and farmers were already weeding them a second time.

[83] In Ghisir: **mimbèndila**. In Eviya: **mimbèndeko**.

[84] As true of many other languages in Gabon (Fang [A.75], Myènè [B.11], Teke [B.71], Ghisir [B.41], Ndzabi [B.52]), there is no word in Tsogho for 'manioc seed', and farmers indifferently called **mibiè mia ghõngo** the flower, the fruit, or the seed.

Tsogho farmers do not weed their fields all at once, but tidy them sector by sector, while sowing peanuts and later while planting manioc, resulting in very patchy distributions of volunteers (Table 4.3). The average density of manioc volunteers in unweeded plots was $2.4 \pm 1.4$ volunteers $\times m^{-2}$, whereas in areas that had already been weeded and planted with manioc, the average density dropped to $0.7 \pm 0.6$ volunteers $\times m^{-2}$. No volunteer was found in manioc farms cleared on 'pristine'[85] forest plots.

**Table 4.3. Density of manioc volunteers in 13 peanuts farms** cleared in September 2007 and partially planted with manioc. The weeding phase of the field is expressed as the percentage of quadrats that fell in a weeded lot.

| Farms | Density/$m^2$ | Weeding phase |
|---|---|---|
| $s_1$ | $0.35 \pm 0.22$ | *100%* |
| $s_2$ | $0.88 \pm 1.02$ | *60%* |
| $s_3$ | $0.30 \pm 0.45$ | *100%* |
| $s_4$ | $1.75 \pm 0.94$ | *40%* |
| $s_5$ | $1.31 \pm 0.78$ | *100%* |
| $s_6$ | $0.85 \pm 1.02$ | *80%* |
| $s_7$ | $1.10 \pm 0.55$ | *80%* |
| $s_8$ | $2.75 \pm 2.38$ | *75%* |
| $s_9$ | $3.40 \pm 1.66$ | *0%* |
| $s_{10}$ | $1.70 \pm 0.41$ | *0%* |
| $s_{11}$ | $1.15 \pm 1.23$ | *60%* |
| $s_{12}$ | $0.90 \pm 0.80$ | *40%* |
| $s_{13}$ | $1.10 \pm 1.24$ | *80%* |
| Average | $1.35 \pm 0.89$ | |

### 2.5.2. Management of seedlings

All farmers in Douani systematically pulled out volunteers from their farms. Manioc volunteer seedlings were perceived as a danger to farmers in Douani. Because there was, they say, a risk that the volunteers are bitter although they resemble sweet landraces, all farmers preferred to discard manioc volunteers. The low quality of the roots produced by volunteers was another frequent explanation for their removal from the farms (Table 4.4).



[85] Caution is needed as to whether the plot was truly pristine. Most likely, the land had been already used, but too long ago for people to remember. There was, however, no evidence of previous land occupation.

**Table 4.4. Farmers' observations and behaviours towards manioc volunteers**.

| Observations, behaviours | Total |
|---|---|
| **Seeds** | |
| Germinate | 15 |
| Do not germinate | 0 |
| **Seedlings** | |
| Have observed volunteers in their own farms | 15 |
| *In peanuts farms (tsete) only* | 13 |
| *In manioc farms (tságha) only* | 0 |
| *In both types of farms* | 2 |
| Have noticed that volunteers appear after burning | 15 |
| *Volunteers originate from old cuttings* | 2 |
| *Volunteers originate from seeds* | 10 |
| *Volunteers originate from both seeds and cuttings* | 2 |
| Allow volunteers to grow | 0 |
| Discard all volunteers | 15 |
| *Roots are not safe to use (bitter)* | 9* |
| *Roots are of poor quality* | 10* |

* Five farmers discarded manioc volunteers both because they generally yield only few roots, and because they sometimes produce bitter manioc.

## 2.6. Sampling strategy

Twenty-four landraces (including three morphotypes) were sampled and genotyped using ten nuclear SSR markers (Table 4.5). The contribution of each farmer to the total sample is shown in Figure 4.2. Samples were collected over the 15 farms surveyed. For each landrace, five samples were collected per farmer, in manioc farms cleared in the previous farming season (September 2006)[86].

Because all farms were by then at least already one year old, they could either be **tságha** farms or former **tsete** farms converted to manioc plantations after peanuts had been harvested. Whether the parcel had previously been planted with peanuts or originally with manioc determines the length of the fallow, and the intensity of weeding. Because this could eventually affect the volunteer densities, and thereby the opportunity for the incorporation of volunteers into the stock of cuttings, I took note of the farming history of the parcel.

[86] At the time of my surveys in Douani, farmers were only starting to plant manioc in their new farms, so there were no leaves for taking samples, and no plants for describing landraces. As the Tsogho have only one cropping season in the year, the most recent farms available for sampling and descriptions were those opened in September 2006.

I identified two categories of farms: (1) **tságha** farms (long fallow, low weeding), and (2) **tsete** farms converted to manioc (short fallow, frequent weeding). Sampling of seedlings was restricted to **tsete** farms opened in the previous month (September 2007). Two cohorts of seedlings ($s_2$ and $s_{13}$) of 29 and 30 individuals, respectively, were sampled from two **tsete** farms[87] and genotyped.

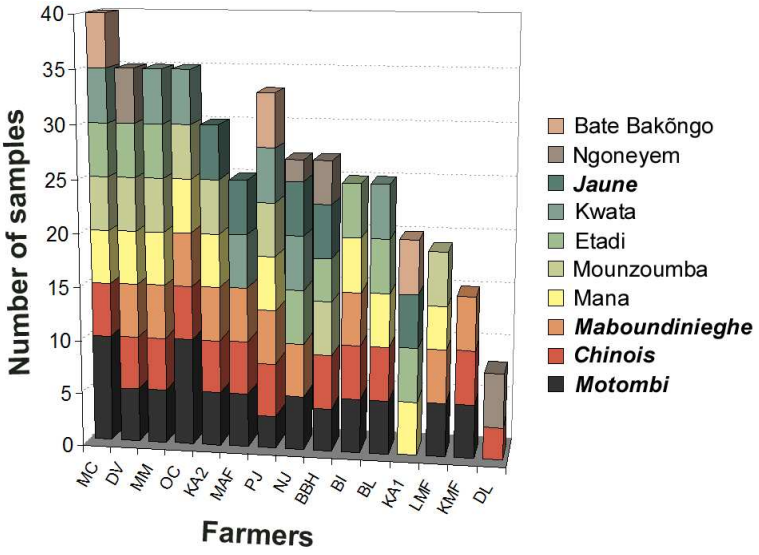



**Figure 4.2. Respective contribution of the 15 farmers to the total sample** (in order of decreasing importance). Because of the high number of named landraces, a lot of which farmers considered as synonyms, only the 10 most common landraces were shown. Four clusters were defined for putative synonyms:

- Bate Bakõngo = '*Bate Bakõngo*' + '*Congo*',
- Maboundinieghe = '*Maboundinieghe*' + '*Simbu*',
- Motõmbi = '*Mutõmbi*' + '*Motõmbi W*' + '*Motõmbi B*',
- Tchosso = '*Dikilikoko Di Jaune*' + '*Iake A Tchosso*' + '*Eakea Tchozo*',
- Chinois = '*Dikilikoko Di Chinois*' + '*Chinois*'+'Jaune' + '*Jaune Chinois*' + '*Iake A Tchosso Chinois*';

The last two clusters, "Chinois" and "Tchosso", were defined on the basis of differences in the colour of the stem: red for the sub-landraces of the "Chinois" cluster, silver for the "Tchosso" cluster.

[87] Both fields, $s_2$ and $s_{13}$, were located in an area already cultivated and left to fallow for two years. Both had been partly weeded and planted with peanuts before sampling took place.

**Table 4.5. Composition of the data set**. The table indicates the number of plants genotyped for each landrace (*N*) as well as the number of farms over which the samples were collected ($N_F$). The table also gives the frequency of the landraces amongst farmers (popularity) and their prevalence (frequency) in the two categories of farms identified according to their farming history. $N_1$ correspond to the number of former tságha farms from which samples were collected, and $N_2$ to the number of former tsete farms. R, B and W stand for "red", "black" and "white", respectively, in accordance with the colour distinction made by farmers between the different morphotypes of '*Iake A Tchosso*' and '*Motõmbi*'. NS stands for "not specified".

| | | | | **Popularity (%)** | **Frequency (%)** | |
|---|---|---|---|---|---|---|
| **Landrace** | | ***N*** | ***N_F*** | ***N=15*** | ***N_1 =11*** | ***N_2 =4*** |
| *Bate Bakõngo* | Bitter | 5 | 1 | *6.7* | *0.0* | *100.0* |
| *Congo* | Bitter | 10 | 2 | *13.3* | *50.0* | *50.0* |
| *Chinois* | Sweet | 15 | 3 | *20.0* | *100.0* | *0.0* |
| syn. *Dikilikoko Di Chinois* | Sweet | 18 | 4 | *26.7* | *75.0* | *25.0* |
| syn. *Jaune Chinois* | Sweet | 10 | 2 | *13.3* | *50.0* | *50.0* |
| syn. *Jaune* | Sweet | 10 | 2 | *13.3* | *50.0* | *50.0* |
| syn. *Iake A Tchosso Chinois* | Sweet | 5 | 1 | *6.7* | *100.0* | *0.0* |
| *Dikilikoko Di Jaune* | Sweet | 10 | 2 | *13.3* | *100.0* | *0.0* |
| syn. *Iake A Tchosso* NS | Sweet | 5 | 1 | *6.7* | *100.0* | *100.0* |
| R | Sweet | 5 | 1 | *6.7* | *100.0* | *0.0* |
| syn. *Eakea Tchozo* | Sweet | 5 | 1 | *6.7* | *100.0* | *0.0* |
| *Etadi* | Sweet | 39 | 8 | *73.3* | *62.5* | *37.5* |
| *Kwata* | Sweet | 35 | 7 | *60.0* | *85.7* | *14.3* |
| *Maboundi* | Sweet | 10 | 2 | *13.3* | *100.0* | *0.0* |
| *Maboundinieghe* | Sweet | 30 | 6 | *46.7* | *100.0* | *0.0* |
| *Mana* | Sweet | 49 | 10 | *66.7* | *70.0* | *30.0* |
| *Motõmbi* NS | Bitter | 47 | 10 | *90.0* | *10.0* | *10.0* |
| W | Bitter | 10 | 2 | *50.0* | *50.0* | *50.0* |
| B | Bitter | 10 | 2 | *50.0* | *50.0* | *50.0* |
| *Mutõmbi* | Bitter | 5 | 1 | *6.7* | *100.0* | *0.0* |
| *Mounzoumba* | Sweet | 40 | 8 | *73.3* | *75.0* | *25.0* |
| *Ndungu* | Bitter | 5 | 1 | *13.3* | *100.0* | *0.0* |
| *Ngoneyem* | Sweet | 16 | 4 | *26.7* | *50.0* | *50.0* |
| *Ngoya* | Sweet | 5 | 1 | *13.3* | *100.0* | *0.0* |
| *Otchaka* | Sweet | 10 | 2 | *26.7* | *50.0* | *50.0* |
| *Pauline* | Sweet | 4 | 1 | *6.7* | *100.0* | *0.0* |
| *Simbu* | Sweet | 20 | 4 | *26.7* | *75.0* | *25.0* |
| Total | | 433 | | | | |

# 3. Genetic diversity in Tsogho farms

## 3.1. Structure of genotypic diversity

Genotypic diversity was analyzed over 433 samples. I identified 32 multilocus genotype (MLG) arbitrarily named G1 to G32, and 29 singletons (Table 4.6). Twenty-three singletons were sampled in **tságha** farms ($N_2$=11), and 6 in **tsete** farms ($N_3$=4). Twenty-four MLGs (75%) were specific to one landrace, and seven (G7, G10, G12, G18, G27, G28, G31) were shared between several landraces. One group (G8) was assigned predominantly to '*Motõmbi*', although the same farmer assigned some G8 plants to '*Motõmbi*', and some other to '*Mana*'.

### 3.1.1. Genotypic characterization of landraces

A few landraces were strictly monoclonal ('*Otchaka*', '*Mana*'). Most of them comprised one clone, dominant, and a few MLGs represented only by a couple of plants (Table 4.7). The analysis of the genotypic composition of landraces confirmed that several of the names given by farmers were in fact synonyms, but also proved wrong some putative synonymies ('*Congo*' and '*Bate Bakõngo*', for example). Landraces with yellow roots formed two clusters with distinct genotypic compositions (Figure 4.3).

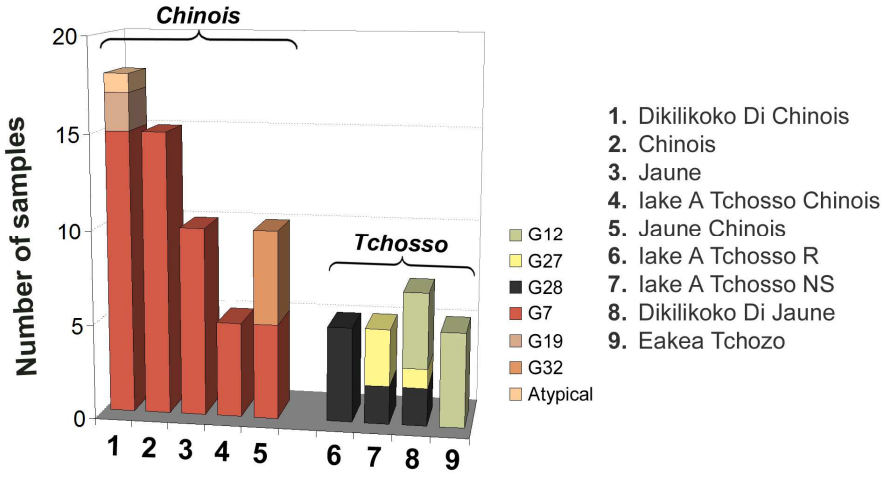



**Figure 4.3. Genotypic structure of the yellow landraces**. While the first cluster, "*Chinois*"', was dominated by one MLG (G7), the second one, "*Tchosso*", consisted of overlapping sub-landraces, and encompassed in total three genotypes (G12, G27 and G28).

Hence, farmers had in total eight different names for only four genotypically distinct yellow root varieties, and in the case of the "Chinois" cluster, up to five different names for the same clone (G7, which represented 78% of the plants of the cluster). 80% (12/15) of farmers grew clones from the "Chinois" cluster, and 40% (6/15) grew clones from the other cluster, "Tchosso". Only three farmers (20%) had cuttings from both clusters.

The diversity of names farmers used for their yellow cultivars reflected a general lack of naming convention between farmers. For example, MAF distinguished '*Dikilikoko Di Jaune*' (Tchosso) from '*Dikilikoko Di Chinois*' (Chinois), while BBH, who also grew '*Dikilikoko Di Jaune*', set it apart from '*Jaune*' (Chinois). $KA_2$, finally, distinguished '*Iake A Tchosso*' (Tchosso) from '*Chinois*' (Chinois). '*Dikilikoko Di Chinois*' and '*Chinois*' were the only two names used by more than two farmers[88].

### 3.1.2. Indexes of agreement

In general, landraces formed consistent genetic entities at the village level (average consistency, $C_F = 87.6\% \pm 12.4$). Mistakes accounted for 4.4% of the sample. Albeit accurate in their identifications, a couple of farmers were in disagreement with all other farmers. Hence, plants identified as '*Kwata*' by MAF, BBH, and OC, had the same multilocus genotype (G18) as plants identified as '*Mounzoumba*' by others. MAF and BBH actually considered the two landraces to be synonyms, but the majority of the farmers in the village did not, and the two names were commonly found together in the farms. In contrast, '*Simbu*' and '*Maboundinieghe*', which many farmers (including MAF) thought to be synonyms, were in fact genotypically distinct. Many farmers confounded one landrace for another, and BBH called '*Etadi*' what all other farmers called '*Motõmbi*'. NJ disagreed with all other farmers, calling '*Simbu*' what most farmers identified as '*Mounzoumba*' and some others identified as '*Kwata*'. Farmer $KA_1$, finally, called '*Mana*' what other farmers called '*Kwata*'. G18 was the major source of disagreement between farmers.

As a result of this lack of a consistent naming system in the village, the average index of agreement between farmers, $OA_j$, was only $79\% \pm 16.2$, ranging from 33.0% for farmer $KA_1$, to 98.2% for farmer DL (266 comparisons).

[88] I found no correspondence between the common use of a particular name and farmers' kinship relationship (see Appendix B2).

**Table 4.6a. Allelic composition of the 32 MLGs identified in Douani** at each of the ten loci studied. The corresponding landrace is also indicated. Alleles are coded with numbers, with the numbers referring to the allele's size (in base pairs) by increasing order*.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| G1 | *Motõmbi* | 1/1 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 5/7 | 3/3 | 4/9 | 2/3 |
| G2 | *Motõmbi* B | 1/1 | 1/1 | 3/3 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 2/6 | 3/3 |
| G3 | *Congo* | 1/1 | 1/1 | 3/3 | 1/6 | 1/2 | 2/4 | 3/5 | 2/3 | 4/5 | 3/3 |
| G4 | *Otchaka* | 1/2 | 1/1 | 2/3 | 1/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/6 | 3/3 |
| G5 | *Simbu* | 1/2 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 1/7 | 5/6 | 2/2 | 2/3 |
| G6 | *Maboundinieghe* | 1/2 | 1/1 | 2/3 | 5/5 | 2/2 | 2/3 | 1/7 | 6/6 | 2/2 | 3/3 |
| G7 | *Chinois* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 3/4 | 1/2 | 3/5 | 2/5 | 3/3 |
| G8 | *Mana* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/1 | 5/6 | 3/9 | 3/3 |
| G9 | *Kwata* | 1/2 | 1/1 | 3/3 | 2/6 | 1/2 | 2/2 | 6/7 | 3/6 | 9/9 | 3/3 |
| G10 | *Motõmbi* B | 1/2 | 1/1 | 2/3 | 2/4 | 2/2 | 2/2 | 3/7 | 5/5 | 4/9 | 2/3 |
| G11 | *Etadi* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| G12 | *Eakea A Tchozo* | 1/2 | 1/1 | 3/3 | 2/5 | 2/3 | 2/2 | 1/1 | 3/5 | 4/9 | 3/3 |
| G13 | *Simbu* | 1/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/2 | 6/7 | 3/5 | 2/6 | 3/3 |
| G14 | *Ngoneyem* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/1 | 3/3 | 2/2 | 3/3 |
| G15 | *Ngoneyem* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 2/9 | 3/3 |
| G16 | *Ndungu* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 3/4 | 2/3 | 4/8 | 2/3 |
| G17 | *Mounzoumba* | 1/2 | 1/3 | 3/3 | 2/5 | 1/1 | 2/4 | 1/5 | 2/5 | 2/8 | 3/3 |
| G18 | *Mounzoumba* | 1/2 | 1/3 | 3/3 | 2/5 | 1/2 | 2/4 | 1/5 | 2/5 | 2/8 | 3/3 |
| G19 | *Chinois* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/2 | 1/1 | 5/6 | 2/9 | 3/3 |
| G20 | *Maboundi* | 1/2 | 1/1 | 2/3 | 6/6 | 2/2 | 2/2 | 5/7 | 2/3 | 6/9 | 3/3 |
| G21 | *Congo* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| G22 | *Pauline* | 1/2 | 1/1 | 3/3 | 2/3 | 2/2 | 2/3 | 1/6 | 3/5 | 2/9 | 3/3 |
| G23 | *Bate Bakõngo* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 5/7 | 2/3 | 5/9 | 3/3 |
| G24 | *Etadi* | 2/2 | 1/1 | 2/2 | 1/6 | 2/2 | 2/3 | 7/7 | 5/5 | 9/9 | 3/3 |
| G25 | *Kwata* | 2/2 | 1/1 | 2/2 | 2/6 | 2/2 | 2/2 | 4/7 | 2/5 | 9/9 | 3/3 |
| G26 | *Mana* | 2/2 | 1/1 | 2/3 | 1/2 | 2/2 | 2/3 | 1/7 | 5/6 | 6/9 | 3/3 |
| G27 | *Tchosso* | 2/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/3 | 1/2 | 4/5 | 5/9 | 3/3 |
| G28 | *Iake A Tchosso* R | 2/2 | 1/1 | 3/3 | 1/2 | 2/3 | 2/3 | 1/2 | 4/5 | 5/9 | 3/3 |
| G29 | *Maboundi* | 2/2 | 1/1 | 3/3 | 2/2 | 2/3 | 2/2 | 1/2 | 3/5 | 2/9 | 2/3 |
| G30 | *Motõmbi* | 2/2 | 1/1 | 3/3 | 3/3 | 2/2 | 2/2 | 7/7 | 3/3 | 2/3 | 2/3 |
| G31 | *Mutõmbi* | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 6/7 | 3/5 | 2/3 | 3/3 |
| G32 | *Jaune Chinois* | 2/2 | 1/1 | 3/3 | 1/1 | 2/3 | 2/2 | 1/6 | 3/3 | 2/4 | 3/3 |

* Corresponding sizes are given in Appendix C3.

**Table 4.6b. Allelic composition of the 29 singletons identified in Douani**.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| 1 | *Bate Bakõngo* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 5/7 | 2/3 | 6/9 | 3/3 |
| 2 | *Chinois* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 3/4 | 1/2 | 3/5 | 2/5 | 3/3 |
| 3 | *Congo* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/1 | 3/6 | 6/9 | 3/3 |
| 4 | *Congo* | 1/2 | 1/1 | 3/3 | 1/5 | 1/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| 5 | *Congo* | 1/1 | 1/1 | 3/3 | 1/6 | 2/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| 6 | *Congo* | 1/1 | 1/1 | 3/3 | 1/6 | 1/2 | 2/4 | 2/3 | 2/3 | 4/5 | 3/3 |
| 7 | *Congo* | 1/1 | 1/1 | 3/3 | 1/6 | 1/2 | 2/4 | 3/3 | 2/3 | 4/5 | 3/3 |
| 8 | *Kwata* | 2/2 | 1/1 | 2/2 | 2/6 | 2/2 | 2/2 | 6/7 | 3/6 | 9/9 | 3/3 |
| 9 | *Kwata* | 1/2 | 1/1 | 3/3 | 2/6 | 1/1 | 2/2 | 6/7 | 3/6 | 9/9 | 3/3 |
| 10 | *Kwata* | 1/2 | 1/1 | 3/3 | 2/6 | 1/2 | 2/2 | 5/7 | 2/5 | 9/9 | 3/3 |
| 11 | *Maboundi* | 1/2 | 1/1 | 2/3 | 6/6 | 2/2 | 2/2 | 5/5 | 2/3 | 6/9 | 3/3 |
| 12 | *Maboundinieghe* | 1/2 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 1/1 | 5/6 | 2/2 | 2/3 |
| 13 | *Maboundinieghe* | 1/2 | 1/1 | 2/3 | 6/6 | 2/2 | 2/3 | 1/7 | 6/6 | 2/2 | 3/3 |
| 14 | *Maboundinieghe* | 2/2 | 1/1 | 2/3 | 2/3 | 2/2 | 2/3 | 1/7 | 3/5 | 9/9 | 3/3 |
| 15 | *Mana* | 1/2 | 1/3 | 3/3 | 2/5 | 1/2 | 2/3 | 1/7 | 5/6 | 6/9 | 3/3 |
| 16 | *Mana* | 2/2 | 1/1 | 2/3 | 1/2 | 2/2 | 2/4 | 1/5 | 2/5 | 2/8 | 3/3 |
| 17 | *Motombi* | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/2 | 6/7 | 3/5 | 2/3 | 3/3 |
| 18 | *Motõmbi* W | 1/2 | 1/1 | 2/3 | 2/4 | 2/2 | 2/3 | 5/7 | 3/5 | 2/2 | 3/3 |
| 19 | *Motõmbi* W | 2/2 | 1/1 | 2/3 | 1/2 | 2/2 | 3/3 | 1/7 | 6/6 | 6/9 | 3/3 |
| 20 | *Mounzoumba* | 1/2 | 1/3 | 3/3 | 2/5 | 1/2 | 2/4 | 1/1 | 2/5 | 2/8 | 3/3 |
| 21 | *Mutõmbi* | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/2 | 3/7 | 5/5 | 4/9 | 2/3 |
| 22 | *Mutõmbi* | 1/2 | 1/1 | 2/3 | 2/4 | 2/2 | 2/3 | 6/7 | 3/5 | 2/3 | 3/3 |
| 23 | *Mutõmbi* | 1/2 | 1/1 | 2/3 | 2/4 | 2/2 | 2/3 | 3/7 | 5/5 | 4/9 | 2/3 |
| 24 | *Ngoneyem* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 9/9 | 3/3 |
| 25 | *Ngoya* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/3 | 6/7 | 3/5 | 2/3 | 3/3 |
| 26 | *Ngoya* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/1 | 3/5 | 6/9 | 3/3 |
| 27 | *Ngoya* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/3 | 6/6 | 3/5 | 2/6 | 3/3 |
| 28 | *Ngoya* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 1/7 | 3/5 | 6/9 | 3/3 |
| 29 | *Ngoya* | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 1/1 | 3/3 | 2/4 | 2/3 |

**Table 4.7. Genotypic composition of Tsogho landraces**. Genotypes were grouped into 'typical', 'non-typical' and 'atypical' categories, according to their distribution amongst landraces. Typical genotypes were either 'specific' when restricted to one landrace, or 'shared' in the case of synonymies. Corresponding number of individuals are also indicated. Consistency of identifications amongst farmers ($C_F$) is given for each landrace, except those that were sampled only over one farm. Plants that showed a genotype typical of another landrace than the one farmers assigned them to were reported in the 'mistaken' column.

| Landraces | | | *N* | Typical | | Non-typical | Atypical | Mistaken | $C_F$ (%) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Specific | Shared | | | | |
| *Bate Bakõngo* | | Bitter | 5 | G23 (4) | — | — | 1 | — | — |
| *Congo* | | Bitter | 10 | G3 (3), G21 (2) | — | — | 5 | — | |
| *Etadi* | | Sweet | 39 | G11 (30), G24 (4) | — | — | — | G26 (1), G31 (3) | *87.2* |
| *Chinois* | | Sweet | 15 | — | G7 (15) | — | — | — | *100.0* |
| syn. *Dikilikoko Di Chinois* | | Sweet | 18 | — | G7 (15) | — | 1 | — | *94.4* |
| syn. *Jaune Chinois* | | Sweet | 10 | — | G7 (5) | — | — | — | *100.0* |
| syn. *Jaune* | | Sweet | 10 | — | G7 (10) | — | — | — | *100.0* |
| syn. *Iake A Tchosso Chinois* | | Sweet | 5 | — | G7 (5) | — | — | — | — |
| *Dikilikoko Di Jaune* | | Sweet | 10 | — | G12 (4), G27 (1), G28 (2) | — | — | G2 (1), G15 (2) | *70.0* |
| syn. *Iake A Tchosso* | NS | Sweet | 5 | — | G27 (3), G28 (2) | — | — | — | — |
| | R | Sweet | 5 | — | G28 (5) | — | — | — | — |
| *syn. Eakea A Tchozo* | | Sweet | 5 | — | G12 (5) | — | — | — | — |

**Table 4.7.** (continued). A particular emphasis was put on G18 (bold) for which there seems to have been much confusion.

| **Landraces** | | ***N*** | **Typical** | | **Non-typical** | **Atypical** | **Mistaken** | ***C*$_F$ (%)** |
|---|---|---|---|---|---|---|---|---|
| | | | **Specific** | **Shared** | | | | |
| *Kwata* | Sweet | 35 | G9 (3), G25 (14) | **G18 (15)** | — | 3 | — | *91.4* |
| *Maboundi* | Sweet | 10 | G20 (4), G29 (5) | — | — | 1 | — | *90.0* |
| *Maboundinieghe* | Sweet | 30 | G5 (22), G6 (4) | — | — | 3 | G31 (1) | *86.7* |
| *Mana* | Sweet | 49 | G26 (37) | — | — | 2 | G8 (5), G11 (1), **G18 (4)** | *79.6* |
| *Motõmbi* W | Bitter | 47 | G1 (5), G30 (4) | G8 (3), G31 (32) | — | 1 | G11 (1), G24 (1) | *93.6* |
| syn. *Motõmbi* | Bitter | 10 | — | G31 (8) | — | 2 | — | *80.0* |
| *Mutõmbi* B | Bitter | 5 | — | G10 (1), G31 (1) | — | 3 | — | — |
| syn. *Motõmbi* | Bitter | 10 | — | G8 (3), G10 (5) | — | — | G2 (2) | *80.0* |
| *Mounzoumba* | Sweet | 40 | G17 (5) | **G18 (34)** | — | 1 | — | *97.5* |
| *Ndungu* | Bitter | 5 | G16 (5) | — | — | — | — | — |
| *Ngoneyem* | Sweet | 16 | G14 (2), G15 (13) | — | — | 1 | — | *100.0* |
| *Ngoya* | Sweet | 5 | — | — | — | 5 | — | — |
| *Otchaka* | Sweet | 10 | G4 (10) | — | — | — | — | *100.0* |
| *Pauline* | Sweet | 4 | G22 (4) | — | — | — | — | — |
| *Simbu* | Sweet | 20 | G2 (5), G13 (9) | — | — | — | G5 (1), **G18 (5)** | *70.0* |

## 3.2. Allelic diversity

Only two alleles ($GA126_{193}$ and $SSR55_{135}$) were rare (frequency <1%). $GA126_{193}$ was restricted to the two morphotypes of '*Motõmbi*' (bitter), and $SSR55_{135}$ was private to '*Tchosso*'. A few alleles were also found to be characteristic of one or the other kind. $SSR31_{178}$ and $SSR31_{168}$ were private to bitter and sweet manioc, respectively. $SSR68_{256}$ was predominantly found among bitter manioc and only in one instance in sweet manioc. $GA57_{185}$ was private to '*Ngoneyem*'.

## 3.3. Overview of genetic diversity in Douani

Table 4.8 shows the values of pairwise differentiation between 14 Tsogho landraces ($N_C \geq 10$). Genetic differentiation between the different components of the two clusters '*Chinois*' and '*Tchosso*' is given in Table 4.9. Between-landraces was the strongest component of genetic variation in Douani ($F_{IT} = -0.119 \pm 0.039$, $P < 0.01$; $F_{IS} = -0.615 \pm 0.024$, $P < 0.01$). All landraces were highly differentiated (average over the loci, $F_{ST} = 0.307 \pm 0.019$, $P < 0.01$). Bitter and sweet maniocs[89] were also clearly differentiated (average over the loci, $F_{ST} = 0.129 \pm 0.02$, $P < 0.01$). Various diversity indexes were computed for each landrace (Table 4.10). Landraces showed strong excess in heterozygotes (except '*Maboundi*'), but moderate levels of allelic diversity (average over the landraces, $A_R = 2.1 \pm 0.349$). Genotypic diversity was low (average over the landraces, $R = 0.176 \pm 0.185$, ranging from 0 for '*Otchaka*' to 0.667 for '*Congo*').



[89] Treated here as pools of landraces.

**Table 4.8. Pairwise genetic differentiation ($F_{ST}$) between 14 Tsogho landraces** (upper-right matrix), and their significance level (lower-left matrix, Benjamini & Hochberg's sharpened test). ** *P*-value < 0.01

| | *Chinois* | *Congo* | *Etadi* | *Kwata* | *Maboundi* | *Maboundinieghe* | *Mana* | *Motõmbi* B | *Motõmbi* W | *Mounzoumba* | *Ngoneyem* | *Otchaka* | *Simbu* | *Tchosso* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Congo* | | 0.368 | 0.297 | 0.275 | 0.234 | 0.189 | 0.404 | 0.434 | 0.218 | 0.300 | 0.277 | 0.291 | 0.303 | 0.217 |
| *Chinois* | ** | | 0.277 | 0.375 | 0.359 | 0.381 | 0.375 | 0.365 | 0.339 | 0.320 | 0.377 | 0.363 | 0.335 | 0.330 |
| *Tchosso* | ** | ** | | 0.239 | 0.190 | 0.163 | 0.355 | 0.256 | 0.190 | 0.278 | 0.290 | 0.313 | 0.408 | 0.285 |
| *Etadi* | ** | ** | ** | | 0.134 | 0.155 | 0.247 | 0.254 | 0.113 | 0.221 | 0.327 | 0.267 | 0.309 | 0.202 |
| *Kwata* | ** | ** | ** | ** | | 0.106 | 0.267 | 0.211 | 0.138 | 0.257 | 0.172 | 0.289 | 0.264 | 0.243 |
| *Maboundi* | ** | ** | ** | ** | ** | | 0.329 | 0.296 | 0.121 | 0.236 | 0.292 | 0.237 | 0.267 | 0.185 |
| *Maboundinieghe* | ** | ** | ** | ** | ** | ** | | 0.316 | 0.236 | 0.253 | 0.358 | 0.352 | 0.370 | 0.261 |
| *Mana* | ** | ** | ** | ** | ** | ** | ** | | 0.250 | 0.320 | 0.414 | 0.410 | 0.391 | 0.380 |
| *Motõmbi* B | ** | ** | ** | ** | ** | ** | ** | ** | | 0.179 | 0.293 | 0.278 | 0.311 | 0.167 |
| *Motõmbi* W | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.342 | 0.258 | 0.319 | 0.138 |
| *Mounzoumba* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.371 | 0.404 | 0.301 |
| *Ngoneyem* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.346 | 0.197 |
| *Otchaka* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | | 0.269 |
| *Simbu* | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | |

**Table 4.9. Pairwise genetic differentiation ($F_{ST}$) between Tsogho 'yellow' landraces** (upper-right matrix), and their significance level (lower-left matrix, Benjamini & Hochberg's sharpened test). $N_C \geq 5$.

| | *Chinois* | *Dikilikoko Di Chinois* | *Iake A Tchosso Chinois* | *Jaune* | *Jaune Chinois* | *Iake A Tchosso* | *Iake A Tchosso* R | *Dikilikoko Di Jaune* | *Eake A Tchozo* |
|---|---|---|---|---|---|---|---|---|---|
| *Chinois* | | 0.009 | 0.000 | 0.000 | 0.191 | 0.332 | 0.364 | 0.363 | 0.512 |
| *Dikilikoko Di Chinois* | *NS* | | 0.007 | 0.005 | 0.12 | 0.259 | 0.292 | 0.278 | 0.409 |
| *Iake A Tchosso Chinois* | *NS* | *NS* | | 0.000 | 0.148 | 0.323 | 0.353 | 0.322 | 0.5 |
| *Jaune* | *NS* | *NS* | *NS* | | 0.178 | 0.329 | 0.36 | 0.349 | 0.508 |
| *Jaune Chinois* | ** | ** | *NS* | * | | 0.269 | 0.276 | 0.198 | 0.294 |
| *Iake A Tchosso* | ** | ** | * | ** | ** | | 0.025 | 0.125 | 0.384 |
| *Iake A Tchosso R* | ** | ** | * | ** | ** | *NS* | | 0.115 | 0.368 |
| *Dikilikoko Di Jaune* | ** | ** | ** | ** | ** | *NS* | *NS* | | 0.057 |
| *Eake A Tchozo* | ** | ** | * | ** | ** | * | ** | *NS* | |

*NS* Not significant, * *P*-value < 0.05, ** *P*-value < 0.01.

**Table 4.10. Diversity statistics computed for each landrace**, after correction for assignment errors (*Nc*). The table shows the number of distinct genotypes in each landrace (*G*), observed ($H_O$) and expected ($H_E$) heterozygosity, $F_{IS}$, allelic richness ($A_R$, averaged over the loci), the number of private alleles ($A_p$), and an index of clonal richness (*R*). Only landraces for which $N_C \geq 10$ were considered.

| **Landrace** | $N_C$ | *G* | $H_O$ | $H_E$ | $F_{IS}$ | $A_R$ | $A_p$ | *R* |
|---|---|---|---|---|---|---|---|---|
| *Congo* | 10 | 7 | 0.580 | 0.393 | -0.434** | 2.3 | — | 0.667 |
| *Etadi* | 35 | 2 | 0.627 | 0.369 | -0.688** | 1.9 | — | 0.029 |
| *Chinois* | 58 | 4 | 0.481 | 0.308 | -0.557** | 2.0 | — | 0.053 |
| *Tchosso* | 22 | 3 | 0.588 | 0.383 | -0.502** | 2.1 | $SSR55_{135}$ | 0.095 |
| *Kwata* | 35 | 6 | 0.541 | 0.459 | -0.162** | 2.5 | — | 0.147 |
| *Maboundi* | 10 | 3 | 0.484 | 0.445 | -0.038 *NS* | 2.3 | — | 0.222 |
| *Maboundinieghe* | 29 | 5 | 0.636 | 0.366 | -0.737** | 1.9 | — | 0.143 |
| *Mana* | 39 | 3 | 0.600 | 0.306 | -0.957** | 1.7 | — | 0.053 |
| *Motõmbi* W | 49 | 6 | 0.575 | 0.381 | -0.732** | 1.9 | — | 0.104 |
| *Motõmbi* B | 19 | 5 | 0.646 | 0.477 | -0.232** | 2.9 | $GA126_{193}$ | 0.222 |
| *Mounzoumba* | 40 | 3 | 0.786 | 0.399 | -0.966** | 1.8 | — | 0.051 |
| *Ngoneyem* | 16 | 3 | 0.662 | 0.346 | -0.886** | 1.7 | $GA57_{185}$ | 0.133 |
| *Otchaka* | 10 | 1 | 0.600 | 0.300 | -1.000** | 1.6 | — | 0.000 |
| *Simbu* | 14 | 2 | 0.571 | 0.375 | -0.501** | 2.2 | — | 0.077 |

*NS* Not significant, * *P*-value < 0.05, ** *P*-value < 0.01.

## 3.4. Genetic diversity of seedlings

### 3.4.1. Allelic diversity

The genetic structure of two cohorts of seedlings, $s_2$ and $s_{13}$, was analyzed[90]. The two cohorts differed slightly in terms of allelic richness (average allelic richness over the loci, $A_R = 3.8$ for $s_2$; $A_R = 3.6$ for $s_{13}$), and were only slightly genetically differentiated ($F_{ST} = 0.049$, $P < 0.01$). $GA126_{193}$, which was only found in bitter manioc ('*Motõmbi*' B), was detected among seedlings collected in $s_2$, but not in $s_{13}$. $SSR31_{178}$ and $SSR68_{256}$, both also private to bitter manioc, were found in the two cohorts. $GA57_{185}$ (private to '*Ngoneyem*'), $SSR31_{181}$, and $SSR55_{135}$, were not detected among seedlings. Conversely, two alleles, $GA57_{183}$ and $SSR31_{191}$, were detected exclusively amongst seedlings[91], but as they were only found in one copy, both could be either recent mutations or typing errors. Volunteer seedlings collected in $s_2$ were issued from geitonogamous pollination (estimated rate of selfing, $s = 0.351$; $CI_{95}(s) = [0.229, 0.440]$), while those collected in $s_{13}$ were not.

### 3.4.2. Parent-offspring analysis

The two cohorts of seedlings ($s_2$ and $s_{13}$) were analyzed through parent-offspring analyses, using the most frequent MLGs (G4, G5, G7, G8, G11, G15, G18, G25, G26, and G31) as potential parents (Table 4.11). Analyses showed that about a third of the seedlings collected in $s_2$ (9/29) were most likely offspring of G11 (typical of '*Etadi*'), and that 9/29 volunteers could be offspring of G26 ('*Mana*'). The majority of volunteers collected in $s_{13}$ (18/30) could be offspring of G18 ('*Mounzoumba*'). Three seedlings in $s_2$ and five seedlings in $s_{13}$ were most likely offspring of '*Motõmbi*' (G31).



[90] Only for nine loci (GA134 did not amplify).

[91] No copies of these alleles were found among the 23 named landraces analyzed, nor in those that were genotyped but not included in the data set ('*Ndungu*', '*Nguya*', '*Pauline*').

**Table 4.11. Parent-offspring analysis of volunteer seedlings collected in $s_2$ and $s_{13}$,** using the likelihood method. The ten most frequent multilocus genotypes were used as potential parents. Only the best LOD score for each seedling was indicated. LOD critical values (3.07 and 1.44, for $P < 0.01$ and $P < 0.05$, respectively) were estimated after 100,000 iterations. Where no *P*-value is associated to the LOD score, no potential 'mother' with a *P*-value below the specified significance levels could be assigned to the seedling. Wherever no potential mother could be found, the MLG column (most likely 'mother') was left blank.

| Volunteers | MLG | LOD | *P*-value | Volunteers | MLG | LOD | *P*-value |
|---|---|---|---|---|---|---|---|
| $s_2$-1 | | -1.35 | | $s_{13}$-1 | | -3.03 | |
| $s_2$-2 | G11 | 1.69 | *< 0.05* | $s_{13}$-2 | G31 | 3.86 | *< 0.01* |
| $s_2$-3 | G26 | 4.21 | *< 0.05* | $s_{13}$-3 | G11 | $9.42 \times 10^{-1}$ | |
| $s_2$-4 | G11 | 2.67 | *< 0.05* | $s_{13}$-4 | G18 | 2.89 | *< 0.05* |
| $s_2$-5 | G18 | 3.91 | *< 0.01* | $s_{13}$-5 | G18 | 3.83 | *< 0.01* |
| $s_2$-6 | G11 | 2.43 | *< 0.05* | $s_{13}$-6 | G31 | 5.43 | *< 0.01* |
| $s_2$-7 | G8 | 3.21 | | $s_{13}$-7 | G18 | $8.23 \times 10^{-1}$ | |
| $s_2$-8 | G11 | 4.41 | *< 0.01* | $s_{13}$-8 | G18 | 4.44 | *< 0.01* |
| $s_2$-9 | G11 | 1.37 | | $s_{13}$-9 | G18 | 3.72 | *< 0.01* |
| $s_2$-10 | G5 | 5.14 | *< 0.01* | $s_{13}$-10 | G31 | 7.66 | *< 0.01* |
| $s_2$-11 | G18 | 2.30 | *< 0.05* | $s_{13}$-11 | G18 | 2.65 | *< 0.05* |
| $s_2$-12 | G26 | 6.50 | *< 0.01* | $s_{13}$-12 | G18 | 4.10 | *< 0.01* |
| $s_2$-13 | G31 | 1.53 | | $s_{13}$-13 | G18 | 1.81 | *< 0.05* |
| $s_2$-14 | G11 | 2.06 | | $s_{13}$-14 | G18 | 3.87 | *< 0.01* |
| $s_2$-15 | G18 | 3.07 | *< 0.05* | $s_{13}$-15 | G18 | 2.81 | *< 0.05* |
| $s_2$-16 | G31 | 3.32 | *< 0.01* | $s_{13}$-16 | G31 | 4.86 | *< 0.01* |
| $s_2$-17 | G31 | 6.32 | *< 0.01* | $s_{13}$-17 | G18 | 2.36 | *< 0.05* |
| $s_2$-18 | G26 | 2.45 | | $s_{13}$-18 | G26 | 5.14 | *< 0.01* |
| $s_2$-19 | G11 | $2.43 \times 10^{-1}$ | | $s_{13}$-19 | G15 | 2.90 | *< 0.05* |
| $s_2$-20 | | $-4.42 \times 10^{-1}$ | | $s_{13}$-20 | G18 | 3.91 | *< 0.01* |
| $s_2$-21 | G11 | 3.26 | *< 0.01* | $s_{13}$-21 | | -3.78 | |
| $s_2$-22 | G11 | $6.38 \times 10^{-1}$ | | $s_{13}$-22 | G7 | 4.99 | *< 0.05* |
| $s_2$-23 | G26 | 4.52 | *< 0.01* | $s_{13}$-23 | G18 | 3.38 | *< 0.01* |
| $s_2$-24 | G26 | 3.40 | *< 0.05* | $s_{13}$-24 | G18 | 3.64 | *< 0.01* |
| $s_2$-25 | G26 | 4.01 | *< 0.05* | $s_{13}$-25 | G26 | 3.41 | |
| $s_2$-26 | G26 | 7.20 | *< 0.01* | $s_{13}$-26 | G18 | 3.08 | *< 0.01* |
| $s_2$-27 | G4 | 1.01 | | $s_{13}$-27 | G31 | 5.62 | *< 0.01* |
| $s_2$-28 | G26 | 3.88 | *< 0.01* | $s_{13}$-28 | G18 | 3.92 | *< 0.01* |
| $s_2$-29 | G26 | 4.76 | *< 0.01* | $s_{13}$-29 | G18 | $8.85 \times 10^{-2}$ | |
| — | — | — | — | $s_{13}$-30 | G18 | 2.04 | *< 0.05* |

# 4. Why grow bitter, why grow sweet?

More than 80% of landraces grown in Douani were "sweet", a disproportion to bitter manioc rarely observed in the Congo region (Jones 1959). The importance of sweet manioc in Douani is in sharp contrast to all other villages I surveyed in Gabon, and to most other African manioc farming systems which have been described (Fresco 1986). Only in East Africa is sweet manioc sometimes preferred to bitter manioc (Jones 1959). Elsewhere, when manioc is the main staple and both types of manioc are cultivated, bitter landraces are generally preferred over sweet ones (Jones 1959, Purseglove 1968, Lathrap 1973, Lancaster *et al.* 1982, Dufour 1993, Nweke *et al.* 1994, 2001, Chiwona-Karltun *et al.* 1998, 2000). Sweet manioc tends to be more important than bitter manioc only in complex cropping systems, where manioc is always a secondary crop (Cousins 1903, Nordenskiöld 1924, Renvoize 1972, Allem 1994, Dufour 1994).

Given the risk of poisoning from incomplete removal of cyanides (Coursey 1973, Rosling 1994, Tylleskär 1994, Cardoso *et al.* 2005), it is difficult to explain why farmers keep growing both bitter and sweet manioc, rather than simply switching to sweet manioc only, and why bitter manioc seems generally favoured by farmers (Fresco 1986). A number of hypotheses have been proposed to explain this seemingly paradoxical choice (Prinz 1988, McKey & Beckerman 1993, Chiwona-Karltun *et al.* 1998, Dufour 1988, Wilson & Dufour 2002).



## 4.1. "Bitter is better"

A recurrent statement in the literature is farmers' belief that bitter manioc is more productive than sweet manioc (Jones 1959, Purseglove 1968, Chernela 1987, Nye 1991), but although de Bruijn (1973) found a small positive correlation between the concentration in cyanogenic glucosides of a landrace and its yield, data from experimental plots are generally inconclusive and somewhat contradictory (for a review, see McKey & Beckerman 1993). In Colombia, Wilson and Dufour (2002) and Wilson (2003) studied the productivity of landraces grown by Tukanoan Indians, and found that bitter manioc, *i.e.*, manioc with high cyanogenic potential, gave higher yields than sweet manioc. In line with McKey and Beckerman (1993), the authors suggest this difference may in fact result from a higher resistance of bitter landraces to pests and diseases. Similar observations were reported for manioc farmers in Cameroon (Poubom *et al.* 2005).

Manioc roots can be left in the ground for up to three years (Jones 1959). Farmers believe bitter manioc to be more resistant to rot, and to be more adapted to live storage, whereas sweet manioc cannot be left in the ground more than a couple of months once roots are mature (Purseglove 1968, Cock 1985). In addition, bitterness confers manioc roots a protection against theft, as their detoxification requires time-consuming processing (Purseglove 1968, McKey & Beckerman 1993, Chiwona-Karltun *et al.* 1998). Another supposed advantage of bitter manioc is that it produces superior quality roots, as compared to sweet manioc (Dufour 1993, Chiwona-Karltun *et al.* 1998), and that the preference for bitter manioc hails from the better quality of products that can be made from it (Nweke 1994, Chiwona-Karltun *et al.* 1998, Wilson & Dufour 2002), but no correlation between starch content and bitterness has been found (see the review in Lancaster *et al.* 1982). In fact, the relative importance of bitter and sweet manioc most often results from cultural preferences (Nye 1991, Emperaire *et al.* 1998, Elias 2000, Rival & McKey 2008), motivated on grounds that cannot solely be accounted for by agronomic performances. In Douani, bitter manioc is depreciated and sweet landraces make up most of the manioc grown in the village[92]. Why did the Tsogho chose to grow mainly sweet manioc, when almost everywhere else in Gabon and in most of Africa and Amazonia, farmers favour bitter manioc?

## 4.2. From farming to logging: the new "gagne-manioc"[93]

### 4.2.1. The trouble with food

Part of the answer lies in the radical socioeconomic changes the Ngounié region experienced at the start of the 20th century. By introducing wage-labour, the fast growing industry of okoumé had created an unprecedented situation, luring farmers away from their plantations, and resulting in a general desertification of villages, starting ca. 1910 and continuing throughout the 1920s (Gray & Ngolet 1999). Hampered by a lack of labour force, agriculture in southern Gabon stalled whilst it had to cope with the thousands of workers gushing to Sindara to join the multiplying lumber camps (Gray 2002). The permanent antagonism of food and wood that ensued from the rapid development of timber industry and the introduction of wage labour in the 20th century was probably the main incentive for the Tsogho to finally adopt manioc as a staple.

[92] It was already the case in the 1960s (see Raponda-Walker & Sillans 1961).

[93] *Lit.* "earn-manioc" (Boucher & Lafage 2000).

From the beginning to the present day, supplying workers with food on lumber camps has been a recurrent problem in Gabon (Bouet 1977, François 1991). Because of their seclusion and the lack of infrastructures, provisioning camps from nearby villages was not a viable option in the long run. A more sensible strategy for workers was to produce food on site (Bouet 1977). Several months, however, are necessary for most crops to yield: three to four for maize, and between 14 and 18 months for plantains. Depending on the varieties, manioc takes between six and 18 months to yield harvestable roots; six to nine for sweet landraces, and 12 to 18 months for bitter manioc (Jones 1959, Silvestre & Arraudeau 1983). Growing sweet manioc is thus a reasonable strategy to ensure substantial yields within a relatively short time. Because manioc farms can produce for two-three years in a row, manioc offers, comparatively to maize and plantains, higher returns for the same amount of work invested in clearing new farms. By growing also bitter manioc, longer to mature but more resistant to rot and compatible with live storage, farmers ensure that, once the farms start producing, there is no break in food production. Fields can then serve afterwards as granaries.

### 4.2.2. The switch to manioc



The Tsogho know several ways to prepare bitter manioc. Like their Ghisir neighbours, the Tsogho also prepare **gari** (**fariña**), but unlike them, and unlike the Myènè (see Chapter III) and the Amerindians (*e.g.*, Elias *et al.* 2000a, McKey & Beckerman 1993, Emperaire *et al.* 1998), the Tsogho use sweet manioc rather than bitter manioc, the latter being almost exclusively prepared in the form of manioc *bâtons*.

For workers on lumber camps, **gari** would have been an appropriate way to solve the recurrent problem of supplying the camp with food. Gari can be stored for several years (Jones 1959), and can be prepared by simply adding water, either hot or cold. In addition, by bringing HCN levels to harmless levels, the preparation of gari would have allowed the use of high-cyanide cultivars. Preparing bitter manioc however engages in a complex series of steps that can take up to one week. Cooking sweet manioc roots is, in contrast, much faster, much simpler, and also very similar to preparing plantains, on which the Tsogho long relied (Raponda-Walker 1952).

Ford (1998) listed several cultural factors that determine the acceptance of a new plant as a food: 1) analogy with indigenous crops, in terms of both cultivation and management; 2) analogy in taste, texture, and processability, which together define 3) the desirability of the new plant.

For populations in need of an easy supply of food, the complexity of preparing gari or manioc *bâtons* was probably initially a curb to the adoption of manioc as a crop. Switching to manioc cultivation was certainly easier with sweet manioc, and only with the introduction from Congo ca. 1920 of varieties of sweet manioc[94], which could be easily substituted for plantains, did the Tsogho really start growing manioc (Raponda-Walker 1945).

With the opening-up of the Tsogho realm in the 1920s, manioc resumed its eastwards diffusion. As factories developed and populations shifted, other populations learned how to plant and how to prepare manioc by cultural impregnation, like the Fang in contact to the Nkomi in the Fernan-Vaz (Sautter 1966). The variety of words Ghisir [B.41], Tsogho [B.31], and Eviya [B.301] use for manioc (**muguma**, **geghõngo**, **kõnga**, or **mopiti**; see Rossel 1987) reflects the cultural exchanges that probably took place at Sindara, a particularly important hub for the populations of southern Gabon in the 1920s (Gray 2002). The mixing of populations may have favoured the transmission of technical innovations, such as the preparation of **gari**, which the Tsogho most likely borrowed from the Ghisir.

In many parts of Africa, including Gabon, colonial authorities introduced and fostered the adoption of sweet manioc varieties (Raponda-Walker 1945, Jones 1959, Fresco 1986). More recently, the CIAM has contributed to the popularisation of improved cultivars developed by the IITA in Ibadan, Nigeria. Reflecting the preferences of Nigerian farmers for sweet manioc, IITA has concentrated efforts on developing sweet cultivars (G. Rossel, pers. comm.).

Significantly, all the most widespread manioc varieties in Gabon ('*Kwata*', '*Matadi*', '*Dame Jaune*', '*Ngoneyem*') are sweet (see neighbour-joining tree in Appendix C3), and most of them are maintained by the CIAM as field genebanks[95]. I suspect many of the



[94] '*Matadi*' was among the landraces R.F Justin Gillet sent between 1920 and 1925 to Mgr. Martrou in Libreville (Raponda-Walker 1945, Raponda-Walker & Sillans 1961). R.F. Gillet founded ca. 1900 the botanic gardens of Kisantu, in DR Congo, where he introduced and multiplied several manioc landraces, and contributed to their diffusion in Gabon. '*Matadi*' is now found across a large part of Gabon under a variety of names ('*Matadi*', '*Ditadi*', '*Etadi*', '*Litadi*'; see Appendix C3). Fresco (1986) also mentions '*Matadi*' as one of the landrace introduced in the late 1970s in the Kwango-Kilu region, in Congo, to palliate a shortage of planting material after a serious outbreak of manioc bacterial blight (caused by *Xanthomonas campestris* pathovar *manihotis* [Berthet et Bondar] Dye).

[95] FAO list of landraces maintained in N'toum (FAO 1995, 2008) mentions '*Kwata*', '*Ditadi*', '*Manioc*

names I recorded in Douani are landraces the diffusion of which was also promoted by the CIAM. One of the sweet landraces grown in the village was even nicknamed '*Ciam*'. The considerable number of sweet landraces accumulated in the village, however, cannot be accounted for only by a recent external encouragement to grow sweet manioc, but stems from cultural grounds, motivated by the socio-economic commotion that followed the development of the timber industry in the region[96].

### 4.2.3. Evolution of farmers' preferences since 1960

Map 4.2 below illustrates the regional and historical variations in terms of relative importance of bitter and sweet manioc, and compares the bitter-sweet ratios recorded by different authors since 1960 in different regions of Gabon where the timber industry has become the principal economic activity. In the 1960s, Raponda-Walker and Sillans (1961) recorded five sweet manioc landraces and three bitter landraces among the Tsogho at Sindara (F on the map). Forty years later, I recorded 21 sweet landraces and only five bitter landraces in Douani (❸). Ghisir farmers' preferences changed, and sweet manioc is now more important around Fougamou (❹) than it was in 1961 (G).

The increase in sweet manioc prevalence around Fougamou coincides with an intensification of forestry activities in the region between 1957 and 1997[97] (OMF 2000), and it is plausible that the former was in fact a consequence of the latter.



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*Jaune*', '*Onenebere*', '*Mambikini*' and '*Ntsut-Mbõng*'.

[96] Adoption of manioc by the Ndzabi [B.52], in the Ogooué-Lolo province, seems to have followed a similar scenario. Until the late 1890s, peanuts and plantains dominated Ndzabi agriculture in Gabon, but only twenty years later, reports mention large Nzabi plantations of manioc (Guillot 1967). In 1912 and 1913, the French waged military campaigns to repress a rebellion of the Ndzabi against colonial authority, and organized a systematic requisitioning of food for rations, provoking food shortages in the villages (Guillot 1970, Dupré 1972). Compelled by hunger, populations had to resort to eat roots from wild yams, some of which highly toxic (*Dioscorea bulbifera* L., Dioscoreaceae), causing several cases of poisoning (Guillot 1967). This troubled period may have favoured the transition to manioc farming, and fostered the adoption of sweet manioc preferentially to bitter manioc. Later, the disruption of the Ndzabi customary farming activities, the enrolment of men in timber yards in the 1930s, then in gold mines in the 1940s and for the exploitation of manganese starting in the 1960s (see Guillot 1970, Dupré 1982) certainly encouraged sweet manioc farming in the Ogooué-Lolo, as it did among the Tsogho in the Ngounié.

[97] The total forest area allocated to concessionary companies increased from 1.6 MHa to 11.9 MHa between 1957 and 1997. Most of this increase (75%) was concentrated in four provinces (Ngounié, Ogooué-Lolo, Ogooué-Ivindo, and Moyen-Ogooué) (OMF 2000).

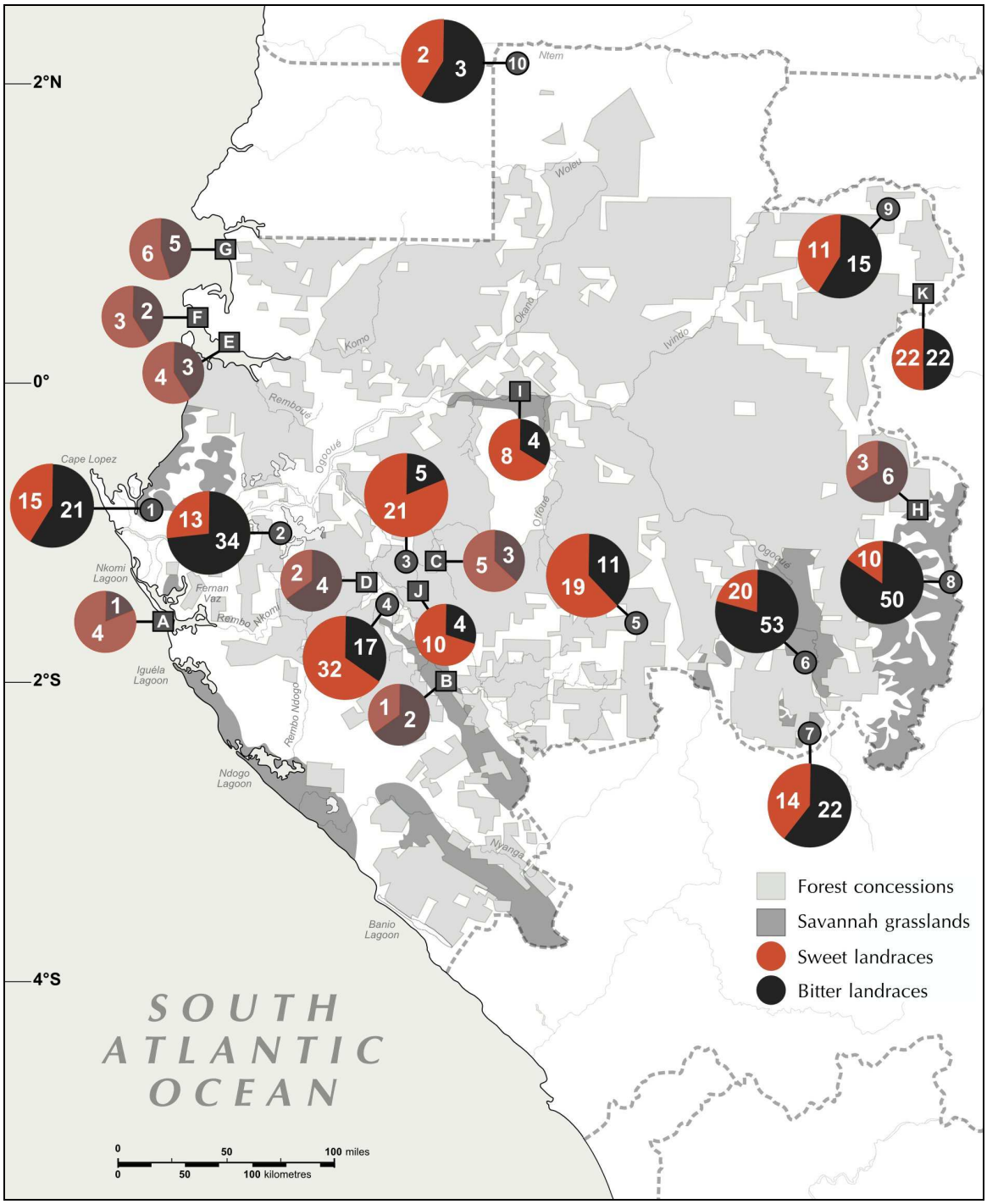
## 4.3. The importance of yellow maniocs

The considerable increase in sweet manioc landraces in Douani since the 1960s confirms that Tsogho farmers have been actively seeking new varieties to grow and have targeted in priority sweet landraces. This predisposition probably explains the popularity of yellow varieties in the region. Elsewhere in Gabon, yellow cultivars account for only a small proportion of the manioc grown. In Mbong-Ete, '*Dame Jaune*' did not catch on because the preparation of manioc *bâtons* requires white varieties, white being associated with a product of high quality (see Chapter V).

Nowhere else in Gabon were yellow maniocs as popular as in Douani. In total, I counted nine different names, and in the farms, yellow cultivars were omnipresent. Genetically, however, I only identified four distinct genotypes (one of which, G7, was dominant), which I grouped in two clusters ("Chinois" and "Tchosso"). A comparison of the genotypes of the different yellow cultivars found in Gabon (see Appendix C3) showed that all landraces from the cluster "Chinois" were clonemates of landraces also found in Mandilou ('*Mutãngani*') and Odimba ('*Ipãndo Jaune*'). Clones from the "Tchosso" cluster, similarly, were found in Mandilou and Makoula ('*Brazzaville*'), and Mbong-Ete ('*Dame Jaune*').

Yellow cultivars are frequent in Amazonia (see Emperaire *et al.* 1998 and references therein), but not in Africa. Breeding varieties with low cyanide and high protein content to enhance the nutritive value of manioc has been for long a priority of research institutes such as CIAT and IITA (Jennings & Iglesias 2002), who have developed and released several sweet yellow cultivars with high carotenoid and amino-acid contents (Iglesias *et al.* 1997, Nassar *et al.* 2009). Between 1970 and 1998, IITA released 206 improved cultivars in Africa, 14 of which were introduced in Gabon (Manyong *et al.* 2000). The popularity of '*Madame Jaune*' is almost certainly the result of massive distributions of cuttings supervised by the CIAM, in charge since the 1970s-1980s with the promotion in Gabon of IITA cultivars.

All yellow varieties were characterized by the unique presence of the allele $GA134_{325}$ (see Appendix C5), which was detected in manioc accessions from Amazonia and French Guiana (see Elias *et al.* 2004, Duputié *et al.* 2009b), but not in Malawi (see Mkumbira *et al.* 2003). $GA134_{325}$ may be the mark of the genetic engineering of varieties with high carotene content by introgression of African cultivars with Amazonian varieties (see Ng & Ng 2002 and references therein).




**Map 4.2. Variation of the relative importance of bitter and sweet manioc** (pie charts) in Gabon and evolution since 1960. The number of landraces categorized as 'bitter' ● and 'sweet' ● is indicated for each of the ten study sites (❶ to ❿). Smaller pies were used for data taken from the literature: **A** (Nkomi [B.11e]), **B** (Apindji [B.303]), **C** (Tsogho [B.31]), **D** (Ghisir [B.41]), **E** (Mpongwe [B.11a]), **F** (Fang Betsi [A.75d]), **G** (Seki [B.21]), and **H** (Mbamba [B.62]) from Raponda-Walker and Sillans (1961). **I** (Kande [B.32]) from Binot (1998); **J** (Eviya [B.301]) from Van der Veen and Bodinga-bwa-Bodinga (2002); **K** (Ngom [B.22b], Mahongwe [B.252]) from Soengas (2010). Wan colours were used for data from the 1960-1980s to contrast with data from the 1990s-2000s. The distribution of forest concessions in Gabon (DGEF 2004) and savannah areas (Caballé & Fontès 1977) are also reported.

### 4.3.1. A discordant naming system

In Douani, yellow maniocs were known to farmers under a variety of names. There was, however, a general disharmony between farmers in Douani in naming manioc landraces. All farmers could accurately differentiate all landraces in their farms, but disagreed with each other when it came to naming them (see Table 4.6). There was in particular a high diversity of names given to yellow cultivars. Farmers were accurate in discriminating between sub-landraces of the two genetic clusters ("Chinois" and "Tchosso"), but none of them had the same convention of naming them, thereby adding to the general confusion in the village. I believe the lack of a consensual naming system at the village level reflects several, independent and relatively recent introductions of yellow varieties in Douani.

### 4.3.2. Low levels of diversity

Despite the confusion of names, landraces in Douani generally formed consistent genotypic entities. Many landraces ('*Otchaka*', '*Mana*', and the sub-landraces '*Jaune*' and '*Chinois*'[98]) were strictly monoclonal. I also found only moderate levels of genotypic diversity, and a low number of singletons (6.7% of the total sample).

With an average of 2.4 manioc volunteer seedlings $\times m^{-2}$ in *tsete* farms, seedling densities were high in Douani. In Guyana, Elias and McKey (2000) found densities of manioc volunteers ranging from 0.04 to 0.48 seedlings $\times m^{-2}$. In French Guiana, Pujol *et al.* (2007) recorded densities averaging 0.39 seedlings $\times m^{-2}$ in newly burned fields. The densities of volunteers recorded in Douani, at least in newly opened **tsete** farms, were five times the values recorded in Amerindian settings. Given such high densities of manioc seedlings, it is a reasonable supposition that a few volunteers escape farmers' vigilance. The relatively low levels of diversity found in Douani, however, suggest that the incorporation of volunteers is happening only at a very low level.

Farmers in Douani had a very low tolerance vis-à-vis manioc volunteers. Manioc seedlings appear at the time they are the least wanted, when it is time to plant peanuts, whose growth they would impede. I found overall fewer singletons in **tsete** farms, reflecting the higher intensity of weeding pressures in this type of farm. But even in manioc farms (**tságha**), manioc volunteers are not desirable, because they produce roots of poor quality, and thus of little interest to farmers.

[98] Also '*Iake A Tchosso*', '*Eake A Tchozo*', '*Pauline*' and '*Ndungu*'.

## 4.4. The importance of *not* being bitter

However, the principal reason why farmers in Douani discarded volunteer seedlings was the fear of poisoning. In all other villages I surveyed, farmers usually discarded seedlings to avoid their competing with cuttings, or because they noticed that volunteers did not reliably produce tuberous roots. In Douani, bitterness was the farmers' main concern, and the poor quality of their roots only came second as an explanation when I asked them why they discarded manioc seedlings.

Parent-offspring analyses suggested that gene flow occurs between bitter and sweet landraces. Both types were mixed in the farms, and the presence of alleles characteristic of bitter manioc ($SSR68_{256}$ and $GA126_{193}$, both private to '*Motõmbi*') clearly indicates that bitter and sweet landraces exchange pollen. The presence of the allele $GA126_{193}$ in the genotype of the volunteers analyzed indicates some degree of relatedness with the landrace '*Motõmbi*'. Although I cannot affirm that the allele $GA126_{193}$ is not also present in a landrace that I have not genotyped, or that I possibly missed out while collecting samples in Douani, it is interesting to note that this allele seems always, in Gabon, associated with bitter manioc (see Appendix C5). $GA126_{193}$ can thus be considered as quasi-diagnostic of bitter manioc, even though the absence of the allele does not, in turn, imply low cyanogenesis.

### 4.4.1. Lability of bitterness in manioc

Manioc bitterness is a very labile character, and the determinants of bitterness in manioc are not yet completely understood. Experimental crosses between manioc cultivars of known toxicity showed that it is also possible to obtain progenies with high cyanogenic potential from sweet parents, and conversely, that sweet phenotypes can arise from crosses between bitter landraces (Valle *et al.* 2004).

Cyanogenesis is regulated by a recessive minor gene complex (Hahn 1973, Mahungu 1994). Using a QTL mapping approach, Kizito *et al.* (2007b) estimated broad-sense heritability ($H^2$) of manioc cyanogenesis to be 43%. However, the genetic determinism of the differentiation between "bitter" and "sweet" manioc is still little documented, and CIAT in Colombia is currently developing a molecular genetic map of manioc (Fregene *et al.* 1997, Fregene & Puonti-Kaerlas 2002, Okogbenin *et al.* 2006), targeting the genes responsible for cyanogenesis in order to develop cultivars with low cyanide content (Jennings & Iglesias 2002).

Several studies have also demonstrated that the cyanogenic potential of a landrace is highly responsive to environmental factors (de Bruijn 1973). Climate, water stress, soil composition, and farming practices (Johns 1990, Bokanga *et al.* 1994) all affect the HCN contents of manioc roots (Sylvestre & Arraudeau 1983, McMahon *et al.* 1995). Cyanogenesis can thus be expressed, or suppressed, depending on changes in ecological conditions, and farmers even reported that on the same plant, roots may have different 'tastes', ranging from "sweet" to "very bitter" (see Chiwona-Karltun *et al.* 1998). Cyanogenic glucosides content (CG) was also shown to vary with the age of the plant (Prinz 1988), particularly in the roots, where CG increases with age (de Bruijn 1973).

Making a clear distinction between "bitter" and "sweet" manioc is thus difficult. Rogers (1965) showed evidence that manioc bitterness evolves along a continuum from one extreme to the other. No morphological character was found to be associated with bitterness (Rogers 1965, Rogers & Appan 1973, Boster 1985b, Nye 1991), possibly because of the independence of morphological traits in manioc (Rogers & Fleming 1973). Yet, manioc farmers generally prove to be accurate in discriminating between their bitter and sweet landraces (Dufour 1988, Chiwona-Karltun *et al.* 1998, 2004, Mkumbira *et al.* 2003, Delêtre & McKey submitted).

Through ideotypic selection (*sensu* Duputié *et al.* 2009), that is, selection based on cultural representation of the 'ideal' phenotype of a landrace, farmers create, at least locally, artificial correlations between the morphological characteristics and the agronomic traits of their manioc landraces, using the former to deduce the latter (Boster 1985). Sexual recombination, however, breaks up those artificial genetic associations, maintained only by strict clonal propagation, and gives alleles a relative independence (Sambatti *et al.* 2001). Manioc volunteers may thus display the morphological characteristics of a sweet landrace, but produce roots with high cyanide content (*e.g.*, de Waal *et al.* 1997).



### 4.4.2. Selection against toxicity

The determinism of bitterness in manioc is governed by a complex set of factors, some genetic but also some ecological, which interact with each others and make the toxicity of manioc volunteers almost unpredictable. In Douani, farmers rejected volunteers mostly by fear of them being toxic.

Fear of food poisoning and the rejection of bitter plants, or those about which farmers are unsure, were already reported by Boster (1984b) among Aguaruna Jívaro farmers in Peru, and by Chiwona-Karltun *et al.* (1998) in Malawi. Peruvian and Malawian farmers both noted that the bitterness of a landrace could be affected by rainfall and soil fertility, but Boster (1984b) noted that Aguaruna Jívaro were rather unconcerned by this plasticity, and Chiwona-Karltun *et al.* (2004) found that Malawian farmers were generally unable to surmise the bitterness of a given landrace even knowing the environment in which it was grown. 'Tasting' the roots thus seem the sole alternative left to farmers to assess the danger of an unknown manioc plant (Chiwona-Karltun *et al.* 1998, 2004). In Peru, farmers wait until manioc volunteers are mature and taste them for bitterness, discarding those with a bitter taste (Boster 1984b).

## 4.5. Toxicity in manioc: between nature and culture

The question of the origins of bitter and sweet manioc has generated a large literature, yet without offering conclusive answers. One hypothesis (Nye 1991) is that the distinction between bitter and sweet manioc is less a biological cleavage between the two kinds than an outcome of cultural differences in preferences for diverse forms of manioc processing. In fact, there is no break in the concentrations of cyanides in manioc landraces. Manioc bitterness evolves along a straight line curve from low to high concentrations in cyanogens (Rogers 1965), and manioc landraces are often categorized into "bitter" or "sweet" based on their processing requirements, rather than from empirical testing of their toxicity (Nye 1991).



Because of the plasticity of bitterness in manioc, and because the range of concentrations in cyanogenic glucosides in cultivated manioc far exceeds that encountered in any wild *Manihot* species, McKey and Beckerman (1993) have proposed a model where cultural preferences have favoured either selection for bitterer or for sweeter varieties (Figure 4.4). In the proposed model, bitterness is artificially selected against or for, depending on the particular use farmers make of manioc roots. Where roots are simply boiled (1), toxic cultivars are too dangerous and are avoided. Artificial selection therefore favours varieties with low levels of toxicity and acts against natural selection[99].

[99] Cyanogenesis has been shown to play an important role in chemical defence in many plants (Jones 1998). In manioc, data are suggestive, but not compelling (McKey & Beckerman 1993, Wilson & Dufour 2002). Cyanogenesis nevertheless contributes to increase the resistance of the roots to non-specialist herbivores

Where flour is the favoured way of preparing manioc, selective pressures against toxicity can be relaxed, because the processing remove cyanides and reduces toxicity to safe levels (Lancaster *et al.* 1982), and nothing opposes natural selection for highly cyanogenic varieties (2). Where there is a strong cultural preference for bitter manioc, as in Malawi (Chiwona-Karltun *et al.* 1998), in Guyana (Elias 2000), or in Colombia (Wilson & Dufour 2002), artificial selection can act in conjunction with natural selection to produce the bitterest varieties (3).

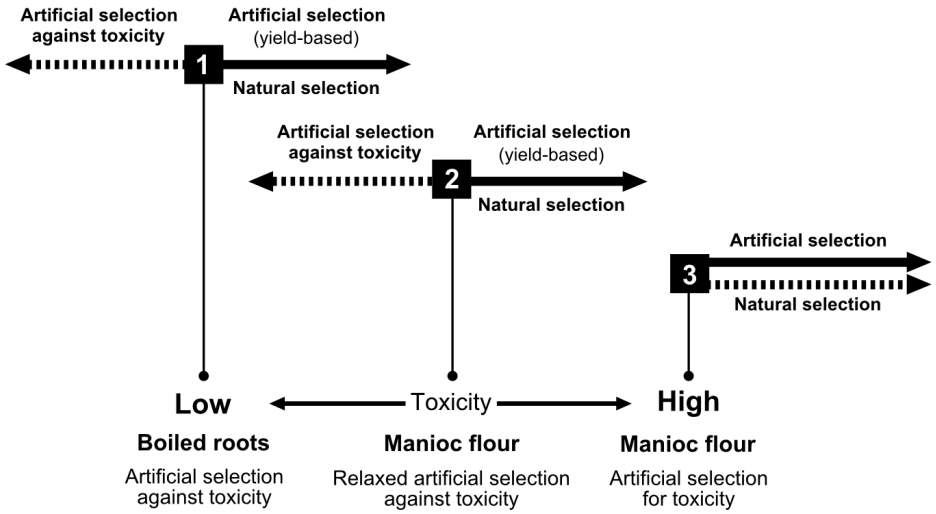



**Figure 4.4. Model of evolution of bitterness in manioc** (adapted from McKey & Beckerman 1993).

McKey and Beckerman (1993) suggested that cultural preferences for a particular preparation of manioc roots are a function of the lifestyle of populations, while Dufour (1996) also underlined the social and cultural aspects of varietal preferences with regard to toxicity. Processing techniques must also be analyzed with regard to the natural and socioeconomic environment of the populations. In Congo, Trèche and Massamba (1996) have shown that preferences for a particular way of preparing manioc, as well as the sequence of the different steps of detoxifying manioc, are parameters that vary among populations depending on their environment and proximity to cities, from which depends their access to markets. The particular case of the Tsogho in Gabon suggests that historical factors, including socioeconomic changes, also govern farmers' choices, and that the preference for bitter or sweet manioc may be also constrained by factors which, ultimately, depend on the context of adoption of the crop.

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(McKey & Beckerman 1993), and natural selection will favour higher cyanogenic manioc where herbivore pressures are high or resource availability is limited.

# 5. Manioc both sides of the Ngounié

For centuries, the Ngounié River has been the natural border between territories of the Tsogho and the Ghisir. Because of the key role the Ngounié played in overland trade in pre-colonial Gabon, it has been, however, more than a physical barrier between the two populations, and to the diffusion of manioc in southern Gabon. The Tsogho and the Ghisir may be geographically close to each other, but there is a cultural and agricultural distance between them that stems essentially from their respective involvement in the troque[100].

## 5.1. Manioc and the troque

Until the first factories were established at Sindara in the 1890s, the Tsogho lingered in the shelter of the Du Chaillu massif, keeping their distance from the agitation of the other tribes, Vili [B.503], Eviya [B.301], Fang [A.75], and Kèlè [B.22], who quarrelled over the control over trade at Samba falls (Gray 2002). Because of this relative seclusion, the Tsogho ignored much of the transformations experienced by other populations of southern Gabon, until colonisation caught up with them at the turn of the century. Opposite the river, the Ghisir, in contrast, were highly involved in trading, possibly because of their key position between the Ngounié River and the Fernan-Vaz lagoon.

Throughout the 18th and 19th centuries, the strong trade connections between the Ghisir and the Myènè Nkomi from Fernan-Vaz had opened way for European goods and for new foods to reach the populations of the interior, and the Ghisir were among the first populations in southern Gabon to adopt European clothing (Raponda-Walker 1960, Gray 2002, Merlet 1991). Along with other items of European manufacture, new crops made their way to the Ngounié. In the 19th century, the Ghisir were particularly renowned for their large plantations of tobacco (du Chaillu, in Merlet 1991, and Raponda-Walker 1960), which the Portuguese had introduced earlier to Gabon[101] (Laufer 1930).

[100] Troque designates the trade of rubber, ivory, raphia, ebony, and slaves, against European manufactured products (gun powder, alcohol, tobacco, fabrics), along a segmented chain of middlemen linking the producers, in the interior, to the dealers on the coast (see Sautter 1966).

[101] Vansina (1985) believes that tobacco cultivation in equatorial Africa started ca. 1700. Tobacco was probably introduced at several places, more or less simultaneously (see Laufer 1930).

Manioc probably followed the same route. Through trade, the Ghisir probably got acquainted with manioc cultivation, and probably started growing manioc about a hundred years before the Tsogho. When du Chaillu visited the region in 1856, manioc was cultivated all along the coast of Gabon and he found it on the left bank of the Ngounié (du Chaillu, in Merlet 1991), but manioc was still completely absent from the opposite side of the river (*ibid.*) where it remained uncommon until the 1910s (Raponda-Walker 1952, Jones 1959).

### 5.1.1. Manioc on the left side of the Ngounié

Farming systems of the Ghisir and the Tsogho are very much alike. Plantains, peanuts and manioc, are central to the Ghisir as they are to the Tsogho, and farmers in Mandilou have distinct types of farms for each crop[102]. As in Douani, sweet manioc prevails in Mandilou. Thirty-two out of the 49 landrace names I recorded in the village corresponded to 'sweet' maniocs. '*Ditadi*', '*Kwata*', '*Simbu*' (all three sweet) and '*Ndungu*' (bitter) were the most popular landraces ($E_f = 0.88$, $E_v = 0.58$). Douani and Mandilou also shared several of their landraces ('*Simbu*', '*Mutõmbi*', '*Ndungu*', '*Ngoya*'), and genetic analyses confirmed several other landraces to be synonyms. '*Ghibadungu*' and '*Otchaka*', '*Brazzaville*' and '*Maboundi*', and '*Mutãngani*' and '*Chinois*', are a few examples among many other synonymies I found between the two villages (Appendix C3). I also found in Mandilou several landraces which I had already found in Odimba, near Port-Gentil ('*Belfutu*', '*Ndzao Re Bimbia*', '*Tãmbroussi*', '*Õmboma*'), but not in Douani.

### 5.1.2. Management of manioc volunteers

Like the Tsogho, Ghisir farmers weed their peanut farms two to three times between September and December, but they were not as zealous in doing so as farmers in Douani, and their behaviour towards manioc volunteers (**mimbèndila**)[103] was more heterogeneous and also somewhat more permissive (Table 4.12). Their motives were also very different from that of the Tsogho.



[102] **Ghiãmba** for plantains (long fallows), and **ghibuga** for peanuts (short fallows). **Ghibuga** farms are usually intercropped with manioc. After peanuts have been harvested, the farms are called **mufunda**.

[103] Densities of manioc volunteers were a little lower in Mandilou than in Douani, ranging from 0.4 to 1 volunteer x $m^{-2}$. However, as the survey took place in November, populations of volunteers probably suffered some mortality, and the values most likely underestimate the actual densities of manioc volunteers in Ghisir agricultural settings.

**Table 4.12. Farmers' behaviour towards manioc volunteers.**

| Observations, behaviours | Total |
|---|---|
| Have noticed that volunteers appear after burning | 18 |
| *Volunteers originate from old cuttings* | 16 |
| *Volunteers originate from seeds* | 2 |
| Allow volunteers to grow | 2 |
| *Known landraces* | 2 |
| Thin volunteers out | 5 |
| *Unknown landraces* | 3 |
| *Known landraces* | 2 |
| Discard all volunteers | 11 |
| *Do not produce roots* | 6 |
| *Known landraces* | 1 |
| *Unknown landraces* | 5 |

Farmers in Mandilou uprooted volunteers mostly to thin out manioc, so that seedlings would not impede the growth of cuttings. Potential toxicity of manioc volunteers was no concern to farmers in Mandilou, and often, farmers would only remove the bulk of manioc volunteers and leave a few behind.

### 5.1.3. Manioc diversity among the Ghisir

Fifteen of the most common manioc varieties were sampled and genotyped (Table 4.13). I identified in total 50 distinct multilocus genotypes (17 MLG groups and 33 singletons; Table 4.14). All MLG groups identified were specific to one landrace. The structure of genotypic diversity endorsed farmers' local taxonomy, which proved accurate and consistent in the village (average $OA_j$ = 93.1% ± 9.9, based on 36 comparisons).

Genotypic diversity also reflected farmers' behaviour towards manioc volunteers. A closer look at genetic diversity in Mandilou (Table 4.13) shows that many landraces were polyclonal. Atypical MLGs accounted for 32.2% of the sample. Singletons were found in almost every farm sampled (Figure 4.5a), and were detected in 12 of the 15 landraces analyzed (Figure 4.5b), suggesting that manioc seedlings contribute to increase the average genotypic diversity of manioc in Mandilou ($R = 0.397 \pm 0.333$), as compared to Douani ($R = 0.176 \pm 0.185$). The difference between the two villages was significant (*t*-test, $t = -2.42$, $n_1 = 129$, $n_2 = 108$, $P < 0.01$).

On one hand, the sampling strategy adopted aimed at maximizing the number of farmers contributing to the sample, and thus possibly biased upwards the values of genotypic diversity. On the other hand, landraces formed consistent entities, with a high index of agreement between farmers. Discrepancies between farmers thus cannot solely account for the levels of genotypic diversity I found in Mandilou.

**Table 4.13. Diversity statistics computed for each landrace** ($N_C \geq 5$). The table indicates the number of plants genotyped for each landrace ($N$) as well as the number of farms over which samples were collected ($N_F$). Sampling strategy was designed to maximize $N_F$. The table also gives the number of distinct genotypes in each landrace ($G$), observed ($H_O$) and expected ($H_E$) heterozygosity, the $F_{IS}$, allelic richness ($A_R$, averaged over the loci), private alleles ($A_p$), and an index of clonal richness ($R$).

| Landrace | $N$ | $N_F$ | $G$ | $H_O$ | $H_E$ | $F_{IS}$ | $A_R$ | $A_p$ | $R$ |
|---|---|---|---|---|---|---|---|---|---|
| *Bata* | 10 | 5 | 7 | 0.800 | 0.547 | -0.420** | 2.9 | — | 0.667 |
| *Brazzaville* | 10 | 4 | 8 | 0.663 | 0.516 | -0.234* | 2.8 | $GA134_{325}$ | 0.778 |
| *Ditadi* | 10 | 5 | 4 | 0.750 | 0.396 | -0.882** | 1.8 | — | 0.333 |
| *Ghibadungu* | 9 | 2 | 1 | 0.569 | 0.300 | -0.885** | 1.6 | — | 0.000 |
| *Kwata Igulu* | 5 | 5 | 2 | 0.300 | 0.280 | 0.040 *NS* | 2.1 | — | 0.250 |
| *Kwata Mayumba* | 9 | 5 | 1 | 0.806 | 0.418 | -0.917** | 1.9 | — | 0.000 |
| *Mutãngani* | 5 | 2 | 2 | 0.500 | 0.250 | -1.000** | 1.5 | — | 0.250 |
| *Mutõmbi* | 9 | 4 | 4 | 0.611 | 0.357 | -0.684** | 2.0 | $SSR68_{256}$ | 0.375 |
| *Ndõng* | 5 | 1 | 2 | 0.823 | 0.493 | -0.610** | 2.4 | $GA57_{185}$ | 0.250 |
| *Ndungu* | 10 | 5 | 6 | 0.650 | 0.419 | -0.512** | 2.5 | — | 0.556 |
| *Ndzao Re Bimbia* | 5 | 1 | 2 | 0.600 | 0.400 | -0.412* | 2.3 | — | 0.250 |
| *Ngungu Remba* | 8 | 2 | 1 | 0.625 | 0.313 | -1.000** | 1.6 | — | 0.000 |
| *Simbu* | 10 | 4 | 10 | 0.738 | 0.546 | -0.303** | 3.0 | — | 1.000 |
| *Six Mois* | 5 | 2 | 2 | 0.500 | 0.250 | -1.000** | 1.5 | — | 0.250 |
| *Timba Jaune* | 5 | 1 | 5 | 0.600 | 0.528 | -0.027 *NS* | 2.6 | — | 1.000 |

*NS* Not significant, * *P*-value < 0.05, ** *P*-value < 0.01.

**Table 4.14. Allelic composition of the 17 MLGs and 33 singletons (●) identified in Mandilou** with the corresponding landraces. Alleles are coded with numbers, with the numbers referring to the allele's size (in base pairs) by increasing order*.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| G1 | *Ndõng* | 1/1 | 1/1 | 3/4 | 1/5 | 1/2 | 2/4 | 1/5 | 3/5 | 2/8 | 1/3 |
| G2 | *Ghibadungu* | 1/2 | 1/1 | 2/3 | 1/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/6 | 3/3 |
| G3 | *Ghibadungu* | 1/2 | 1/1 | 2/3 | 1/6 | 2/2 | 2/4 | 5/7 | 3/3 | 6/6 | 3/3 |
| G4 | *Brazzaville* | 2/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/3 | 1/5 | 4/5 | 5/9 | 3/3 |
| G5 | *Mutãngani* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 3/4 | 1/2 | 3/5 | 2/5 | 3/3 |
| G6 | *Ndungu* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/6 | 3/5 | 6/9 | 3/3 |
| G7 | *Ndungu* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/6 | 3/5 | 5/9 | 2/3 |
| G8 | *Ditadi* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| G9 | *Kwata Mayumba* | 1/2 | 1/3 | 3/3 | 2/2 | 1/1 | 2/4 | 1/5 | 2/5 | 2/8 | 3/3 |
| G10 | *Kwata Mayumba* | 1/2 | 1/3 | 3/3 | 2/5 | 1/2 | 2/4 | 1/5 | 2/5 | 2/8 | 3/3 |
| G11 | *Ndzao Re Bimbia* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 1/2 | 5/7 | 2/3 | 5/9 | 3/3 |
| G12 | *Bata* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 5/7 | 2/3 | 6/9 | 3/3 |
| G13 | *Bata* | 1/2 | 1/1 | 3/3 | 1/5 | 2/2 | 2/4 | 1/5 | 3/6 | 6/9 | 3/3 |
| G14 | *Kwata Igulu* | 2/2 | 1/1 | 2/2 | 2/6 | 2/2 | 2/2 | 1/6 | 2/5 | 9/9 | 2/3 |
| G15 | *Six Mois* | 2/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/3 | 1/5 | 2/3 | 9/9 | 3/3 |
| G16 | *Brazzaville* | 1/2 | 1/1 | 2/3 | 1/6 | 2/3 | 2/3 | 2/6 | 4/5 | 2/6 | 3/3 |
| G17 | *Mutõmbi* W | 2/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 6/7 | 3/5 | 2/3 | 3/3 |

* Corresponding sizes are given in Appendix C3.

**Table 4.14.** (continued)

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| ●1 | *Bata* | 1/2 | 1/1 | 2/3 | 2/3 | 2/2 | 2/3 | 1/5 | 1/3 | 2/2 | 3/3 |
| ●2 | *Bata* | 1/1 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 1/5 | 3/5 | 2/5 | 2/3 |
| ●3 | *Bata* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/3 | 5/7 | 2/3 | 5/9 | 3/3 |
| ●4 | *Bata* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 5/7 | 2/3 | 5/9 | 3/3 |
| ●5 | *Brazzaville* | 1/2 | 1/1 | 2/3 | 1/6 | 2/3 | 2/3 | 2/6 | 4/5 | 2/5 | 3/3 |
| ●6 | *Brazzaville* | 1/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 1/5 | 3/3 | 2/5 | 2/3 |
| ●7 | *Brazzaville* | 2/2 | 1/1 | 2/3 | 1/2 | 2/2 | 1/2 | 7/7 | 2/5 | 5/9 | 3/3 |
| ●8 | *Brazzaville* | 1/1 | 1/1 | 3/3 | 2/6 | 1/2 | 2/2 | 7/7 | 2/3 | 9/9 | 3/3 |
| ●9 | *Ditadi* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 1/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| ●10 | *Ditadi* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/2 | 1/7 | 3/5 | 2/2 | 3/3 |
| ●11 | *Ditadi* | 1/2 | 1/1 | 2/2 | 2/5 | 2/2 | 1/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| ●12 | *Kwata Igulu* | 1/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/2 | 1/5 | 3/3 | 2/6 | 3/3 |
| ●13 | *Mutõmbi* W | 1/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/3 | 1/1 | 3/5 | 6/9 | 2/3 |
| ●14 | *Mutõmbi* W | 1/2 | 1/1 | 3/3 | 2/3 | 2/2 | 2/3 | 6/7 | 3/5 | 2/5 | 3/3 |
| ●15 | *Ndungu* | 1/2 | 1/1 | 3/3 | 2/4 | 2/2 | 2/3 | 1/1 | 3/5 | 6/9 | 2/3 |
| ●16 | *Ndungu* | 1/2 | 1/1 | 3/3 | 2/5 | 2/2 | 1/2 | 1/3 | 2/5 | 8/9 | 2/3 |
| ●17 | *Ndungu* | 2/2 | 1/1 | 3/3 | 1/2 | 2/2 | 2/3 | 1/1 | 3/5 | 6/9 | 2/3 |
| ●18 | *Ndungu* | 1/2 | 1/1 | 3/3 | 2/4 | 2/2 | 2/3 | 1/3 | 3/5 | 5/9 | 2/3 |
| ●19 | *Ndungu* | 1/2 | 1/1 | 3/3 | 4/5 | 2/2 | 2/3 | 1/6 | 3/5 | 2/6 | 2/3 |
| ●20 | *Simbu* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/3 | 1/7 | 2/5 | 4/5 | 3/3 |
| ●21 | *Simbu* | 1/1 | 1/1 | 3/4 | 1/5 | 1/1 | 2/3 | 1/7 | 3/5 | 4/5 | 2/3 |
| ●22 | *Simbu* | 1/2 | 1/1 | 2/3 | 4/5 | 2/2 | 2/3 | 1/7 | 5/6 | 2/2 | 2/3 |
| ●23 | *Simbu* | 1/2 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 1/7 | 5/5 | 2/2 | 2/3 |
| ●24 | *Simbu* | 1/2 | 1/1 | 3/3 | 4/5 | 2/2 | 1/2 | 6/7 | 3/5 | 2/6 | 3/3 |
| ●25 | *Simbu* | 1/2 | 1/1 | 3/3 | 2/4 | 2/2 | 2/2 | 6/7 | 5/5 | 4/9 | 3/3 |
| ●26 | *Simbu* | 1/2 | 1/1 | 3/3 | 3/5 | 2/2 | 2/2 | 6/7 | 3/5 | 2/5 | 3/3 |
| ●27 | *Simbu* | 1/2 | 1/1 | 2/3 | 4/5 | 2/2 | 2/3 | 1/7 | 3/5 | 2/6 | 3/3 |
| ●28 | *Simbu* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/3 | 1/7 | 1/5 | 2/6 | 3/3 |
| ●29 | *Timba Jaune* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 3/4 | 1/2 | 3/5 | 4/4 | 3/3 |
| ●30 | *Timba Jaune* | 1/2 | 1/1 | 3/3 | 1/1 | 2/2 | 2/3 | 1/2 | 3/5 | 4/4 | 3/3 |
| ●31 | *Timba Jaune* | 1/2 | 1/3 | 2/3 | 5/6 | 1/1 | 2/2 | 5/7 | 2/3 | 4/9 | 3/3 |
| ●32 | *Timba Jaune* | 1/2 | 1/3 | 2/3 | 5/6 | 1/2 | 2/2 | 5/7 | 2/3 | 4/9 | 3/3 |
| ●33 | *Timba Jaune* | 1/2 | 1/1 | 2/3 | 2/5 | 2/2 | 2/2 | 1/7 | 3/5 | 9/9 | 3/3 |

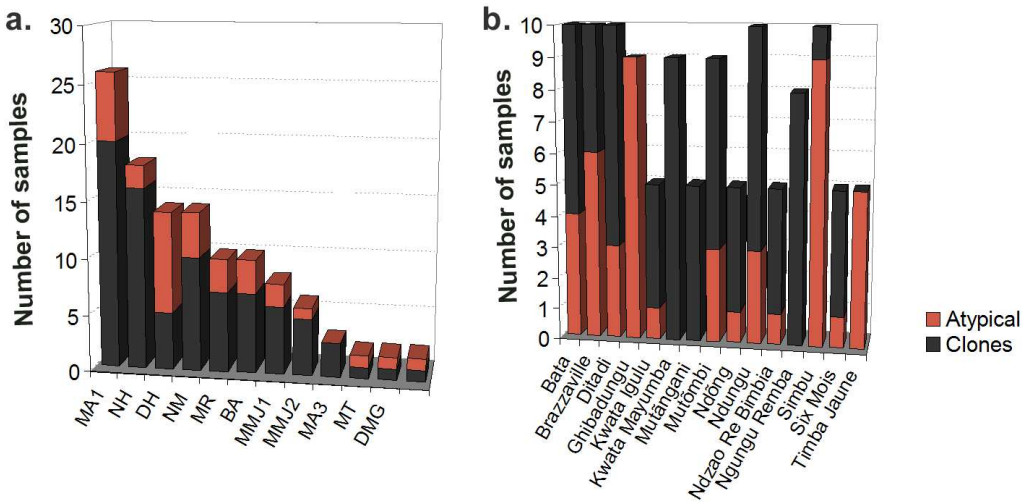



**Figure 4.5. Relative proportion of atypical MLGs per farmer** (a) **and per landrace** (b).

## 5.2. Orungu, Galwa, n'Eshira: obot'omo[104]

Douani and Mandilou are only 30 km distant. Yet, culturally, the Ghisir have always been closer to the Myènè [B.11] than they have been to the Tsogho. From the time they left the Bas-Congo region (Van der Veen 2001) and migrated northwards to Lake Ogemoué, near Lambaréné, the Ghisir have always been close to the Myènè. Even after they retreated to the savannahs of southern Gabon in the early 18th century (Raponda-Walker 1960), the Ghisir resumed their contact with the Nkomi [B.11e] at Fernan-Vaz and Sette-Cama, and the Galwa [B.11c] around Lake Onangué (Sautter 1966). The two different versions of the oral tradition of the Myènè concur on this close tie between Myènè and Ghisir (Raponda-Walker 1960, Merlet 1989).

Long and repeated periods of cohabitation between Ghisir and Myènè have favoured the transmission of elements of the Myènè material culture[105], including manioc cultivation. From the Myènè, the Ghisir have learned how to plant[106] and how to prepare manioc, and with them (and to a lesser extent with the Tsogho), the Ghisir are indeed the only tribes in Central Africa to prepare the **fariña**, a method otherwise restricted to West Africa (Jones 1959, Lancaster *et al.* 1982).

[104] "Orungu, Galwa, Eshira: Same father" (Ghisir proverb).

[105] Sugarcane wine (**mussungu**) is also known only to the Ghisir and the Myènè (Gaulme 1981).

[106] This is a remarkable detail, as in all other populations I surveyed in Gabon, planting techniques—the number as well as the disposition and orientation of manioc cuttings—were a very distinctive trait of manioc farming among a particular ethnic group. Like the Myènè, Ghisir farmers bury cuttings horizontally, and cover them with soil.

The Myènè probably learned the preparation of **fariña** in contact with the Portuguese (Sautter 1966; see also Chapter III), and the Ghisir most likely learned it from the Myènè, before they passed it on (much later) to the Tsogho. The importance of the cultural influence of the Myènè on the Ghisir is well illustrated in the different ways Ghisir and Tsogho farmers manage manioc diversity in their farms, and is above all reflected in their management of manioc volunteers. Gari (**fariña**) is popular in Mandilou. Because the technique is efficient in removing cyanide, toxicity is not a constraint anymore, and pressures on seedlings can be relaxed. Significantly, not one farmer in Mandilou mentioned the risk of manioc volunteers being poisonous.

Although several studies have considered the basis and accuracy of traditional taxonomies of manioc landraces into bitter and sweet (Chiwona-Karltun *et al.* 1998, Mkumbira *et al.* 2003), the hypothesis of bitterness being a result of the combined effects of agroecological factors and farmers' selection has been little tested in the field. Studying the cyanogenic potential of manioc volunteers and variations among societies in regard to practices pertaining to their inclusion would certainly offer interesting insights into the origins of bitter and sweet manioc.



**Synthesis**

Triggered by the exploitation of okoumé, the onset of manioc farming in southern Gabon was intricately linked to the pending threat of a Malthusian crisis in Gabon in the 1910-1920s. For the colony and for the populations, manioc appeared as a solution to the permanent antagonism of food and wood production. For want of knowledge of more elaborate ways to prepare manioc, the Tsogho have developed a preference for sweet manioc, which could be easily substituted for plantains. Although they have since learned other techniques, they still hold a preference for sweet manioc and practice a strong selection against toxicity, systematically rejecting manioc volunteers, thereby maintaining low levels of genotypic diversity despite the high densities of manioc volunteer seedlings in their farms. Ghisir farmers, in contrast, have discovered manioc in contact with the Myènè, and learned from them efficient ways to detoxify manioc, allowing them to relax pressures on manioc volunteers. Hence, a simple difference of preferences for a form of preparation of manioc indirectly influenced farmers' management of diversity.





**Plate IV**

Unlike their Ghisir neighbours, who plant manioc in a way very similar to that of the Myènè (a), the Tsogho plant manioc stem cuttings (**pende**) in triads. Two cuttings are planted diagonally, parallel to each other, opposing a third one which is planted in the middle (b).

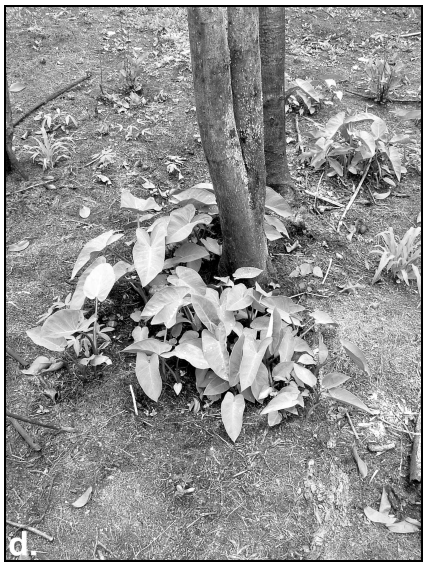





**Plate IV** (continued)

Tsogho farmers weed their fields sector by sector (c), while sowing peanuts and later while planting manioc. They spare yam and taro volunteers (d), but manioc volunteers (**midènga**) are treated as weeds and systematically discarded (e).

# Chapter V

## *"In the midst of manioc"*

**Mbong-Ete**
02°08'17.9"N, 011°29'56.7"E
*Fang Ntumu (A.75a)*

# Abstract

Varietal impoverishment often follows when the non-utilitarian dimensions of diversity (kinship, heritage, aesthetics, and sociality) give out to economic incentives, and when yield becomes farmers' main concern. Several authors have noticed a tendency among manioc farmers to reduce the number of landraces they maintain in their farms as the importance of the crop as a source of revenue increases (Salick *et al.* 1997, Emperaire *et al.* 1998, McKey *et al.* 2001, Manusset 2006, Heckler & Zent 2008).

In this chapter, I contemplated another example of a staggering 'deviation' from the generally large numbers of manioc landraces maintained by farmers in Gabon. In the Woleu-Ntem (northern Gabon), the Fang Ntumu [A.75a] know only eight different names for manioc landraces. Whether this low diversity reflects a cultural choice, a stern selection of the most productive landraces dictated by the strong market orientation of manioc farming in the region, or simply a lack of useful diversity, was explored through an analysis of the political and economic evolution of the Woleu-Ntem in the 19$^{th}$ century's "scramble for Africa".

# 1. The latecomers: the Fang expansion in the 1850s

In Gabon, the Fang [A.75] (Guthrie 1948, Maho 2003) form a large, homogeneous ethnic cluster that extends from the Ntem River, in northern Gabon, as far as Libreville, to the west, and Lambaréné, to the South (Map 5.1). Most of northern Gabon is occupied by the Fang Ntumu [A.75a], whose territory spreads from the river Woleu, in Gabon, to the river Ntem and beyond, in Cameroon and Equatorial Guinea.

## 1.1. Origins of the Fang

The Fang (often confused with the Pahouins[107]) originated from the Sanaga valley, in central Cameroon (Murdock 1959, Perrois 1972, Chamberlin 1978, Vansina 1990). Their installation in Gabon (see Appendix A2) is contemporaneous with the establishment of European trade factories on the Gabon estuary (Chamberlin 1978). The Fang probably left the Sanaga valley around 1790[108], moving southwards to the Ntem and the Woleu, in present northern Gabon (Alexandre 1965, Perrois 1972). After a short hiatus, their migration resumed in Gabon in the mid-19th century.

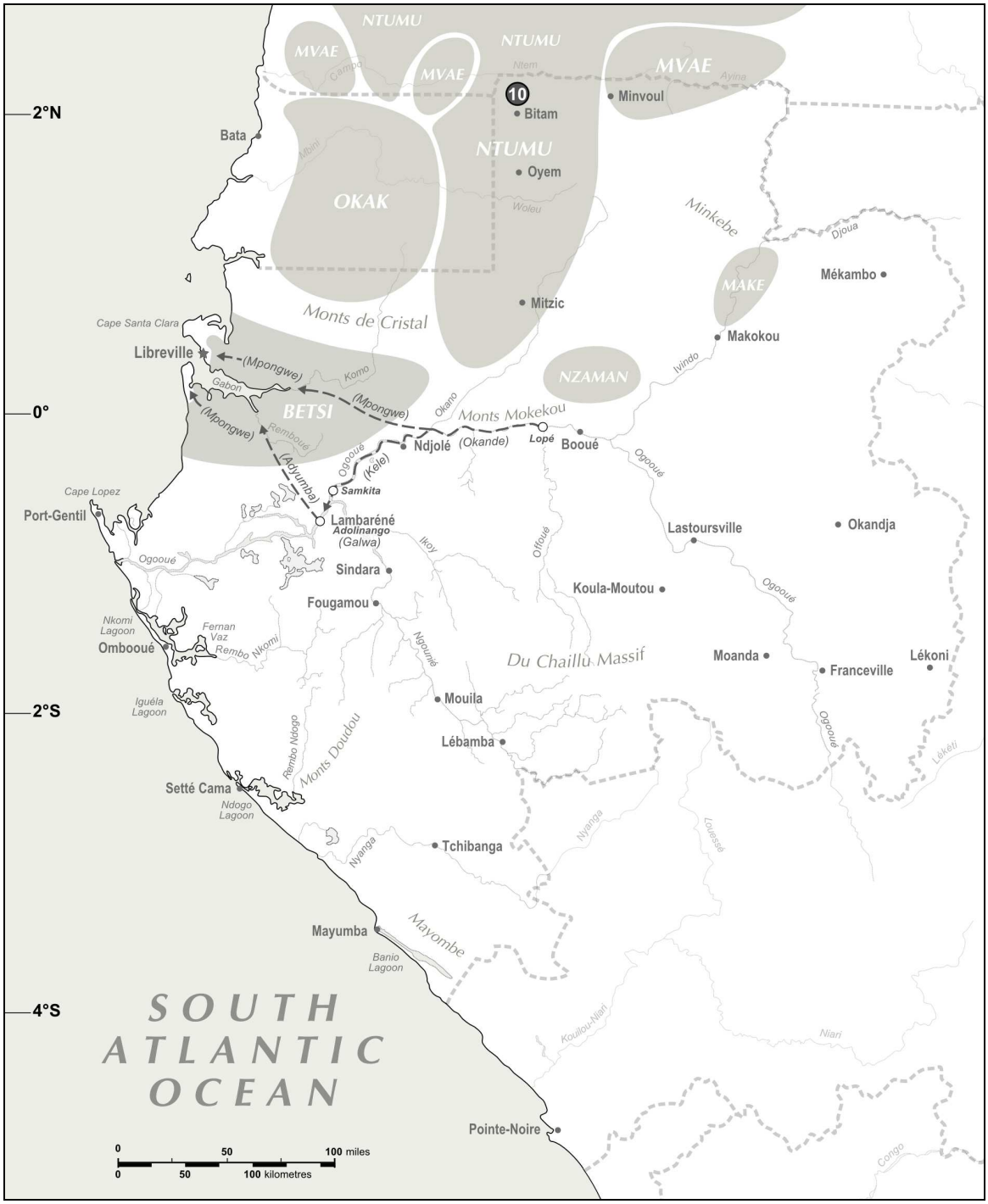
Little by little, the Fang loomed towards the coast between 1840 and 1860[109], absorbing gradually the Seki [B.21] and the Kèlè [B.22] in the upper Komo, and replacing the Mpongwe [B.11a] on the Gabon estuary. They finally reached the Fernan-Vaz, the southernmost limit of their expansion, in 1897 (Merlet 1990a).

In the last phase of their migration, their main driving force was the desire of the Fang to establish direct trading contacts with European merchants established on the Gabon estuary (Chamberlin 1978, Cadet 2009). The appeal of European manufactured goods (**bium**) encouraged the Fang to get closer to the coast, and to settle in proximity to administrative posts and trading centres (Chamberlin 1978, Bernault 2003).

[107] Pahouins actually refers to a larger geographical cluster of culturally related ethnic groups, the Beti [A.65], the Bulu [A.74] and the Fang. Among the Fang, linguists distinguish the Ntumu [A.75a], the Okak [A.75b], the Make [A.75c], the Betsi [A.75d], the Nzaman [A.75e], and the Mvae [A.75f].

[108] The actual timing of the migration is controversial. Some authors believe the Fang to have emigrated from Cameroon as early as the 15th or 16th century (Vansina 1990). Alexandre (1965) and Balandier (1970) believe the Fang left the Sanaga valley under the pressure of the eastward expansion of the Fulani (large nomadic group from West Africa), in the 18th century.

[109] First, in the 1840s, the Fang Betsi from the Monts-de-Cristal, then, in the 1860s, the Fang Make from northern Gabon (Chamberlin 1978).




**Map 5.1. Present distribution of the Fang across Gabon, Cameroon and Equatorial Guinea** (adapted from Perrois 1972 and Maho 2003). The Ntumu [A.75a] represent the majority in Gabon and occupy most of the Woleu-Ntem. In the 1850s, the Fang made a bid for the control over trade routes linking Lopé, Samkita and Lambaréné (arrows), displacing the Okande [B.32] at La Lopé, the Mpongwe [B.11a] and the Kèlè [B.22] in the estuary, and the Galwa [B.11c] around Lambaréné. The location of Mbong-Ete ❿ is reported on the map.

## 1.2. The Fang, the French and the Germans

Ever since the migration of Fang through Cameroon to Gabon, the Woleu-Ntem has remained exclusively Fang[110], and constituted an area of very strong ethnic homogeneity with low to no penetration by other cultures. During their migrations, the Fang converted other populations to their culture rather than the opposite, through an assimilation process that ethnographers called "pahouinisation" (Raponda-Walker 1960, Merlet 1990a, Dounias 1993). It is this apparent dynamism that persuaded the French administration, in the early hours of colonisation, to encourage the rapprochement of the Fang as potential partners for the future development of the colony (Bernault 2003). However, relations rapidly stiffened. The Fang rebelled against the political and economic coercion of the French colonial authority[111] (*ibid.*). Unable to assert its authority on local populations, and unable to control a territory disputed by Germany[112], the French government engaged in a policy of intimidation and occupation of northern Gabon, which durably affected the social and economic organisation of Fang societies.

### 1.2.1. The creation of Woleu-Ntem: 1907

With the occupation of Cameroon by Germany in 1884, the delimitation of German and French possessions in Equatorial Africa became a regular source of contention. In 1885, France and Germany ruled on the partition of the Woleu-Ntem, but frictions were still frequent on the border. In 1901, France and Germany agreed to observe a s*tatus quo* on the boundaries between Cameroon and Gabon, until France ordered, in 1906, a geographical mission to delimit the borders of Cameroon and Gabon and finally put an end to German intrusions in their colonial possessions (Cadet 2009). The next year, boundaries of Cameroon, Gabon and Congo were materialised by milestones. The region of Woleu-Ntem was officially created on the 15th of February, 1907 and stations were created in Oyem, Bitam and Minvoul.

[110] In the Woleu-Ntem, the Fang still represent 99% of the population (Joiris & Bahuchet 1994).

[111] Adopted in 1881, the "Code de l'indigénat" instated forced labour, with imprisonment for those who tried to escape it. It was generalized in 1887 to all French colonies and was abolished only in 1946. In 1897, the French administration also introduced a poll tax. Refusing to pay, villages fled back into the forest to escape taxation (Cadet 2009).

[112] Northern Gabon had become a key region for industrial activities (wood, rubber), and attracted the covetousness of concessionary companies, in particular the Société commerciale, industrielle et agricole du Haut-Ogooué (S.H.O.), and the Gesellschaft Süd Kamerun (G.S.K.) (Cadet 2009).

### 1.2.2. World War I in Gabon: 1914-1916

This respite did not last long. In 1912, the French government conceded the Woleu-Ntem back to Germany to settle a dispute over Morocco. But when, only two years later, the turmoil of World War I reached African colonies, the Woleu-Ntem became again the theatre of violent clashes between France and Germany, waging war over the control of northern Gabon. After the defeat of Germany in 1916, France and Great Britain agreed on a partition of Cameroon, and the Woleu-Ntem came back into French custody.

Eager to finally stabilize the area, the new colonial authority took a series of reforms aiming at the political and economic subjugation of the populations (Bernault 2003, Knight 2003), notably through the compulsory creation of farming communities ("*paysannats*") and by expanding the production of cacao (Dounias 1993, Bernault 2003, Cadet 2009).

### 1.2.3. The great famine: 1916-1925

With the increasing demand of the colonial state for men, employed on farming estates and lumber camps in the middle Ogooué (Balandier 1950, Sautter 1966, Gray & Ngolet 1999), this new policy encouraged a rural exodus and aggravated male depletion in villages (Bernault 2003), already greatly affected by the mandatory enrolment of men as soldiers during World War I (Gray 2002). Lacking a labour force to clear new plantations, villages all around the region suffered from regular food shortages, resulting in a general famine in the 1920s (Sautter 1966, Gray & Ngolet 1999).

In an attempt to handle the general food crisis, the colonial administration ordered the resettlement of villages along roads in a final attempt to fix communities[113], and implemented new agricultural policies[114], encouraging villages to develop local farming (Sautter 1966, Knight 2003) and fostering the adoption of manioc as a staple (Jones 1959). It is in the context of this policy that the village of Mbong-Ete was relocated along the road now linking Oyem and Bitam, in Gabon, to Ambam and Ebolowa, in Cameroon.



[113] *Décret du 22 février 1910 du mouvement vers Libreville*. See also Carrière (1999).

[114] *Arrêté du 31 Décembre 1920*, which made work on large communal plantations mandatory. The food was to provision cities and workers on construction sites. See Guyer (1978).

## 1.3. Mbong-Ete

Mbong-Ete (02°08'17.9"N, 011°29'56.7"E) is a Ntumu community of about 40 households (ca. 200 people), located ten kilometres north of Bitam, in the Woleu-Ntem province, northern Gabon. The etymology of the name of the village, "Mbong-Ete", epitomizes the history of the Woleu-Ntem, and reflects the complete transformation of the ethnic, social and agricultural landscape of Gabon in the early hours of colonisation.

### 1.3.1. The history of Mbong-Ete

Originally lying east of its current location, the village, then known as Mimbang-Alèn ("oil palm", *Elaeis guineensis*), was relocated in the 1920s, during the great famine, as part of the French policy to regroup villages along roads. The colonial authority was, at that time, trying to bolster agriculture in the region, in order to supply Oyem and Bitam with farm products. When the new location of the village was decided, the local authorities ordered the creation of large collective manioc plantations, and farmers were supplied with cuttings. When the people from Mimbang-Alèn started opening farms in their new village and to plant manioc, the soil was so fertile that the village soon became, literally, surrounded by manioc. That's where the name of the village came from. In Ntumu, **mbong-ete** means "in the midst of manioc".

### 1.3.2. Surveys

Surveys were conducted in Mbong-Ete in September 2006. Twenty-eight farmers[115], all Ntumu, participated in the survey. Although the majority of farmers I interviewed were born in Gabon, a high proportion were natives of Cameroon (29%) or Equatorial Guinea (11%), and only seven farmers (25%) were born in Mbong-Ete.



[115] See typology of farmers in Appendix B1.

# 2. Agriculture among the Ntumu

Little is known about early agriculture among the Fang, although there is little doubt that the Fang were already practicing slash-and-burn agriculture by the time they left the Sanaga valley, in the 18th century (Vansina 1990, Mbot 1997, Cadet 2009). Linguistic evidence and the persistence in several "pahouin" or "pahouinised" societies of structures destined for the storage of yams attest that yams (*Dioscorea dumetorum*, *D. cayennensis-rotundata*, *D. minutiflora*, *D. alata*) were originally the dominant crop among the Pahouins[116] (Murdock 1959, Dounias 1993). However, with the introduction of crops of Asian and American origin, yams quickly lost ground, supplanted by plantains in the 17th century, and afterwards by maize and manioc, in the 19th century. Taro and macabo (*Xanthosoma sagittifolium* [L.] Schott, Araceae) also completed, later, the range of crops usually found in Fang farms.

## 2.1. The spread of manioc among the Fang

Precisely how and when the Fang started to grow manioc is still obscure. The Fang epopee, as recounted by the chief of Ayeng, Nkoro, to Father Trilles in 1894, does not mention manioc among the staples of their ancestors. Manioc and maize, it seems, were not known to the Fang until long after the beginning of their migrations, in the first half of the 18th century, and the Fang were by then mainly growing bananas (Merlet 1990, but see also Miracle 1965). The only certainty about manioc in northern Gabon is that it was still unknown to the populations until late in the second half of the 19th century (Murdock 1959), and that its diffusion, in this part of Gabon, was probably hastened by the penetration of Europeans in Africa (*ibid.*, see also Prinz 1988).

If manioc spread throughout Gabon along trade routes, as it probably did in most of central Africa (Murdock 1959), then the Fang, who for long had been the "castoffs" of the flourishing trade on the Gabon estuary, probably did not learn about manioc until they moved closer to the coast.



[116] Beti, Bulu and Fang confounded.

### 2.1.1. First contact: Betsi and Make

Manioc probably spread among the Fang beginning around the 1860s. Writings of missionaries suggest that manioc was grown by the Fang in the estuary after 1865, although its cultivation may have been encouraged by the missionaries themselves (see for example Raponda-Walker 1960 and Merlet 1990), as it was later by the colonial authorities (Jones 1959).

Manioc probably followed two routes. It diffused first from the estuary and along the Ogooué, and the first Fang migrants (Betsi [A.75d] and Make [A.75c]) most likely familiarized themselves with manioc cultivation through contact with other populations, as they drew nearer to the coast. Support for a first contact mediated by the Seke [B.21] is given by an analysis of the vernacular names of pineapple (*Ananas comosus* [L.] Merr., Bromeliaceae). Pineapple, a Brazilian fruit, was probably introduced to West Africa and São Tomé in the 16th century (Raponda-Walker 1952). In Myènè [B.11], pineapple is called **ikoko ni atãnga**[117], "the sugar of the Whites". Betsi and Make call it **nkoc-sec**, "the sugar of the Seke". Linguistic evidence hence suggests that Betsi and Make discovered the pineapple in contact with the Seke, probably when they migrated in the 1840s-1860s. In contrast, the Fang Ntumu [A.75a] and Mvae [A.75f] did not know pineapple in 1900. Tessmann (1913) did not mention it in his description of the Fang[118] crop portfolio, and linguistic evidence[119] suggests that pineapple followed another route to reach northern Gabon.

### 2.1.2. Second contact: Ntumu and Mvae

In northern Gabon, Ntumu and the Mvae did not start growing manioc before European penetration in the 1890s. The diffusion of macabo (*Xanthosoma sagittifolium* [L.] Schott, Araceae), another root crop introduced from Jamaica to Africa through Fernando Pô in 1842 (Ardener 1956), suggests the diffusion of new crops may have been slowed down by the relative lack of connection between the populations of the interior and populations on the coast. Until about 1880, Ntumu and Mvae still ignored macabo (Tessmann 1913), and the second contact of the Fang with manioc probably did not occur before the introduction in the German Cameroons of sweet manioc varieties imported from the Carribean islands (Mouton 1949).



[117] See Chapter III.

[118] Ntumu [A.75a] and Mvae [A.75f].

[119] In Ntumu, pineapple is called **zègˈ**; in Mvae, **ayãng**.

## 2.2. The Ntumu farming system

The Ntumu distinguish a short and a long rainy season, although the two seasons differ not so much in length but mainly in the intensity of rainfalls (Figure 5.1). The transition from the dry season to the rainy season is the signal to start a new farming cycle. Twice a year, farmers clear large forest plots, which are later divided into smaller parcels of approximately half a hectare, and redistributed between families.

### 2.2.1. Agricultural calendar

The farms (**afup**, pl. **mofup**) must be burnt before the first rains. The Ntumu distinguish three different kinds of farms: **afup ekone** (①), where farmers only grow plantains, **afup mbõng** (②), where manioc is grown in association with maize, and **afup owono** (③), where they grow mainly peanuts which they later intercrop with manioc.

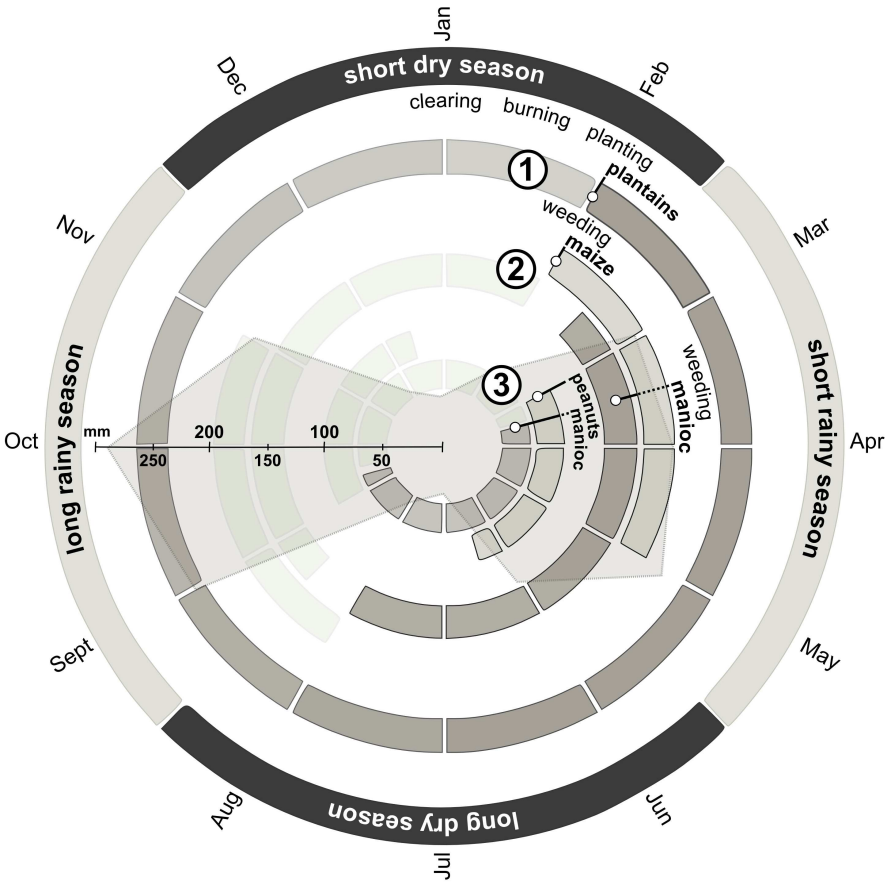



**Figure 5.1. The Ntumu agricultural calendar**. Farmers open new farms twice a year, in January and July. Because the two seasons follow exactly the same scheme, only one farming season was represented on the figure. Distribution of rainfalls (radar diagram) is also indicated.

### 2.2.2. Composition of Ntumu farms

The Ntumu portfolio of crops is large (Table 5.1) and also includes a large variety of "greens" (**edng**). The "greens" category embraces a broad variety of plants, either cultivated or naturally occurring in the wild and favoured by farmers in their farms[120]. Manioc, maize, peanuts and bananas are the main staples in Mbong-Ete. Macabo is not very popular in Mbong-Ete. It is seldom found in Ntumu farms, and is planted mainly in orchards in the village, behind houses. Formerly, farmers also grew rice (*Oryza glaberrima*), but they reported that they abandoned the crop in the 1960s.

**Table 5.1. Composition of Ntumu farms in Mbong-Ete**. Manioc, maize, sugarcane, peanuts and bananas (both types) were the most commonly cited crops (frequency > 50%).

| Crop | Latin name | Vernacular name |
|---|---|---|
| Aubergines | *Solanum* spp. | **zõng** |
| Avocadoes | *Persea americana* | **fie** |
| Bananas | *Musa acuminata** | **adjí** |
| Beans | *Phaseolus vulgaris* | [121] |
| Gombos | *Abelmoschus esculentus* | **etètam** |
| Maize | *Zea mays* | **fone** |
| Manioc | *Manihot esculenta* | **mbõng** |
| Onions | *Allium cepa* | **agnõn** |
| Oseille | *Hibiscus sabdariffa* | **essãng** |
| Peanuts | *Arachis hypogaea* | **owono** |
| Peppers | *Capsicum* spp. | **odõndo** |
| Pineapples | *Ananas comosus* | **zèg** |
| Plantains | *Musa sapientum* var. *paradisiaca*** | **ekone** |
| Pumpkins | *Cucurbita maxima* | **abog** |
| Spinaches | *Amaranthus* spp. | **folõng** |
| Squashes | *Cucumeropsis mannii* | **ngone** |
| Sugarcane | *Saccharum officinarum* | **nkoc** |
| Sweet potatoes | *Ipomoea batatas* | **dogo** |
| Taros | *Colocasia esculenta* | **ekaban** |
| Tomatoes | *Lycopersicon esculentum* | **okoumogoro** |
| Yams | *Dioscorea* spp. | **zogo** |

* AA group; ** ABB group.

[120] The greens (in French, "brèdes") group of plants are grown for their leaves and used either for cooking or for medicinal purposes. They comprise several species of the genus *Amaranthus* and *Solanum*.

[121] The Fang have no word for "bean", possibly because of the lack of similitude with any of their traditional crops (see Raponda-Walker 1945).

### 2.2.3. Fallows

In comparison to the rest of the country, population density is high in the Woleu-Ntem, greater than 10 persons x $km^{-2}$ around Oyem and Bitam (Appendix A4). Pressures on land impose a short turn-over of agricultural land. Fallows (**ekoro**, pl. **bikoro**) rarely exceed 10 years, and last on average three to five years. To maintain soil fertility, farmers in Mbong-Ete alternate, every year, the zone they put under cultivation, and clear new farms either west or east of the village[122]. Whether the parcel will be sown with plantains, peanuts or manioc, then depends on the quality of soil, which is determined by the length of the fallow (Figure 5.2).

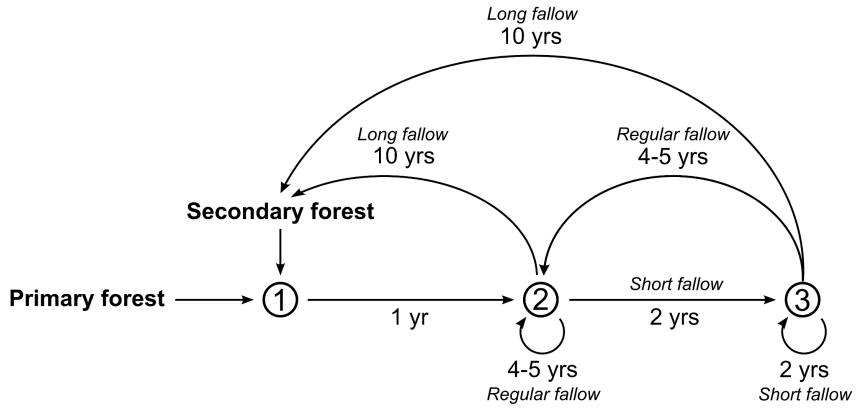



**Figure 5.2. Relation between length of fallow and land occupation**. On primary forest, farmers grow plantains (1). After harvest, the plot is left fallow for one year, then cleared again and converted to a manioc plantation (2). After two years fallow, it can be used for planting peanuts (3). If the fallow lasts longer (four to five years), the plot is again planted with manioc. If the fallow exceeds 10 years, the plot can be planted again with plantains.

On a plot which was never cleared before, or where the fallow exceeded ten years, the Ntumu will only grow plantains, which need a soil rich in nutrients but do not require any particular soil preparation after burning. After harvest, the plot is left to fallow for one year, then cleared again and used to grow manioc.



[122] Within the boundaries of each household's respective agricultural domain (in conformity with customary law; see Bahuchet & de Maret 1994). Rules of land appropriation among the Ntumu specify that by clearing a piece of land, farmers become *de facto* the landowners (Carrière 1999). Karsenty *et al.* (1997) called this custom the "*occupatus*". It also gives the farmers a pre-emptive right over the land surrounding their parcels ("*arcfinus*", *sensu* Karsenty *et al.* 1997).

Peanuts, on the contrary, need a perfectly clean soil, and farmers spend a long time after burning to weed their fields and remove any roots or branches left after clearing. To reduce the time and effort required to clear the plot, farmers only grow peanuts in farms which have been left fallow for two or three years, and where vegetation has not grown too big yet. Manioc is generally grown on plots that have remained for four or five years in fallow. Farms planted with manioc as the sole staple however tend to be rare, and manioc is almost always intercropped with peanuts.

Peanuts are ready for harvest after three months and maize after two months. Manioc is generally ready after six months, but the harvest of manioc can be spread over two-three years, depending on the size of the farms, and how resistant landraces are to live-storage[123].

## 2.3. Manioc

Manioc is the principal source of revenue of farmers in Mbong-Ete. Every week, each household processes ten to fifteen bundles of *bâtons de manioc*[124] (**ndãla-mbõng**). Sold for 1,000 FCFA the bundle of ten *bâtons* on the market in Bitam, manioc represents a weekly income of 10,000 to 15,000 FCFA for the farmers.

Most manioc grown by farmers in Mbong-Ete mature in six to eight months, so that the first set of farms are ready for harvest by the time the second cropping season starts. In this way, farmers stagger food supply, providing fresh roots all year long. Bitter manioc predominates in Fang farms. Sweet manioc has little commercial value and is grown principally for household needs.

### 2.3.1. Planting pattern

Manioc landraces are usually organised in large mono-varietal plots. Single stem cuttings, measuring between 40 and 55 cm in length for 2-2.5 cm diameter, are planted diagonally, with two-thirds being covered up with soil. Manioc cuttings are planted approximately one metre apart, and an average-sized field of half a hectare may contain up to 5,000 plants.



[123] That is, leaving the roots in the ground long after the plant reached maturity.

[124] Each bundle is made of ten manioc *bâtons*, and weighs approximately 5kg.

### 2.3.2. Productivity

The yield per hectare was estimated on a series of five measures of the fresh weight of roots. '*Esobo-Nku*', the most widespread and the most cultivated landrace, yielded on average 5 kg per stalk, which represents about 50 tons of fresh roots per hectare[125], a production similar to that obtained with improved cultivars (Cock 1985). Usually, half the field area was planted with '*Esobo-Nku*', a third with the landrace '*Adzoro*', and the rest with sweet manioc.

## 2.4. Embedded varietal diversity

In comparison to the other villages I surveyed, the number of named landraces I recorded in Mbong-Ete was surprisingly low (Table 5.2). All farmers grew the same set of three landraces ($E_v = 0.99$ and $E_f = 0.99$), which also appeared to be common to other villages in the environs, including parts of Cameroon and Equatorial Guinea[126].

Farmers cited two bitter landraces, '*Adzoro*' and '*Esobo-Nku*'. They mentioned also several landraces of sweet manioc ('*Afouba-Mbõng*', '*Akwama-Mbõng*', '*Matati*', '*Dame Alice*'), all of which appeared however to be synonyms. One farmer also distinguished different morphotypes of '*Matati*', on the basis of variations of the colour of the leaves. I chose to differentiate the four morphotypes in the analyses by adjoining them a letter; *a* for the most widespread morphotype, *b*, *c* and *d* for the three variants.

### 2.4.1. Origin of landraces

According to my informants, '*Adzoro*' and '*Afouba-Mbõng*' (otherwise known as '*Akwama-Mbõng*') are the two oldest, original Ntumu landraces, which their parents and grand-parents before used to grow. '*Esobo-Nku*' and '*Matati*' were apparently introduced in Mbong-Ete in the 1920s, when the colonial administration, eager to end food shortages in the region, fostered manioc cultivation and provided villages with cuttings.



[125] Estimated total yield, based on an average production of 5 kg per manioc stalk and a planting density of one stalk/$m^2$ (10,000 plants/ha, see Leihner 2002). No data are available for other landraces.

[126] Women born in Cameroon and Equatorial Guinea were asked about the landraces grown in their village of origin, and invariably cited the same three landraces.

**Table 5.2. Distribution of named manioc landraces** (rows) **among farmers** (columns) **in Mbong-Ete**. 'x' indicates where the landraces were found.

| Landraces | | | NAM | NZG | $NEI_1$ | EM | NMC | EC | MH | MMJ | AAL | BZS | NOL | NMM | OL | AOB | OOI | AE | BP | NOG | EOJ | AJ | NMJF | AMT | ONJ | ZAM | OZJ | AEV | $NEI_2$ | MET |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Esobo-Nku* | | Bitter | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x |
| *Adzoro* | | Bitter | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | x | | x | x | x | x | x | x | x | x | x | x |
| *Nkot-Mbõng* | | Bitter | x | | | | | x | | | | | | | | | | | | | | | | | | | | | | |
| *Akwama-Mbõng* | | Sweet | | | | | | | | x | | x | x | | | x | x | x | | | | x | x | | x | | x | x | | |
| syn. *Afouba-Mbõng* | | Sweet | | | | x | x | x | x | | x | | | | | | | | | x | | | | x | | | | | x | x |
| syn. *Dame Alice* | | Sweet | | x | x | | | | | | | | | | | | | | | | | | | | | | | | | |
| syn. *Matati* | a | Sweet | x | | | | | | | | | | | x | x | | | | x | | | | | | | x | | | | |
| | b | Sweet | x | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | c | Sweet | x | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | d | Sweet | x | | | | | | | | | | | | | | | | | | | | x | | | | | | | |
| *Dame Jaune* | | Sweet | x | | | | | | | | | | | | | | | | | | | | x | | | | | | | |

Occasionally, farmers also mentioned '*Nkot-Mbõng*' ("dry manioc") and '*Dame Jaune*' as landraces they grew, but these never accounted for more than a few cuttings maintained in a corner of a field. '*Dame Jaune*', very popular in the rest of the country, was introduced in Mbong-Ete about five years ago, but was unsuccessful. Farmers prefer landraces with white roots, more suitable for the preparation of manioc *bâtons*[127]. '*Nkot-Mbõng*' is not a landrace *per se*, but refers to volunteers that farmers missed while weeding their farms, and that produce a single tap root with high fibre content. '*Nkot-Mbõng*' is considered of low quality.

### 2.4.2. Transmission of landraces

Unlike most communities in Gabon where landraces are usually transferred from mothers to daughters (vertical transmission), among the Ntumu cuttings are given to the daughter-in-law by her mother-in-law. Affinal[128] transmission represented 74% of the exchanges of landraces in Mbong-Ete (Figure 5.3).

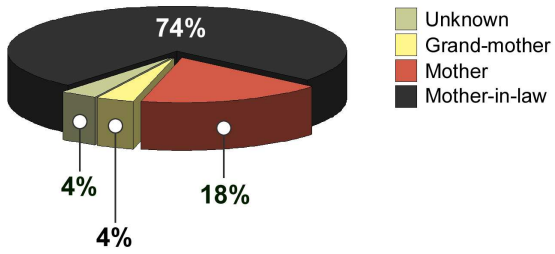



**Figure 5.3. Transmission of landraces in Mbong-Ete**.

### 2.4.3. Morphological diversity

Because of the limited number of distinct landraces, the range of morphological diversity is rather limited in Mbong-Ete, but landraces display distinctive phenotypic characteristics that allow farmers to spot them immediately in their farms. Stem colour and colour pattern of the petiole, particular to each landrace, make their identification unambiguous and confusion virtually impossible. Farmers sometimes also use fruits as a criterion for discriminating between landraces.

[127] The white colour of manioc *bâtons* is a very important criterion of quality, as it is an indicator of the freshness of the product.

[128] "Affinal" derives from "affine", and characterizes any relationship by means of marriage in general, by opposition to "kin" which designates individuals related by descent. In the present case, it is specifically used to designate the relation between a woman and her daughter-in-law.

All Ntumu landraces produce flowers and fruits, and farmers noticed that each landrace produces fruits with a different colour pattern. The most striking difference between landraces is the colour of the torus, at the base of the fruit. Orange for '*Adzoro*', it is red for '*Dame Jaune*', yellow for '*Matati* a', purple for the morphotype '*Matati* d', and green for '*Esobo-Nku*'.

Farmers also reported differences in plants' architecture between landraces. Unlike the other landraces which grow tall (up to 3-4 metres) and branch off tardily, the primary stem of '*Adzoro*' divides early on, leading to an overall smaller plant, at maturity, but a higher branching level (Figure 5.4). '*Adzoro*' architecture is so unusual and characteristic of the landrace that the name '*Adzoro*' ("the small") reflects this difference.

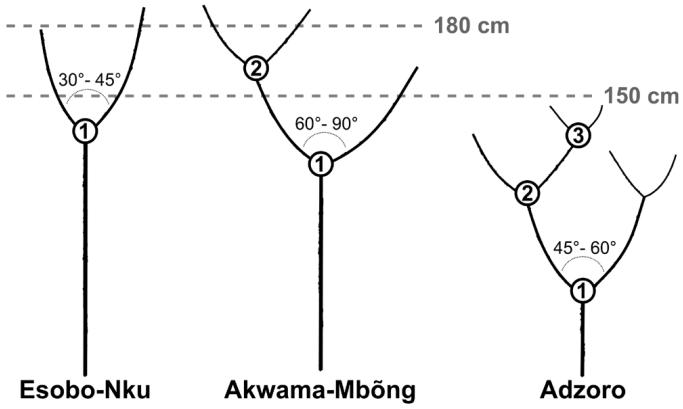



**Figure 5.4. Schematic representation of architecture of Ntumu landraces**, based on morphological descriptions. The angle of the first ramification as well as the degree of ramification, given as the number of successive di- or trichotomous divisions of the stem, are indicated. For '*Esobo-Nku*', '*Akwama-Mbõng*' and '*Adzoro*', the percentage of non-ramified stems was between 81-100%, 0-20%, and 0-20% respectively. Heights (150 and 180 cm) are based on the mean sizes measured in the field on mature plants ($N = 5$).

## 2.5. Manioc volunteers

In old farms (planted in February or August 2005), many plants bore mature fruits, and seeds were found in great quantity on the ground[129]. I conducted censuses and exhaustive collections of manioc volunteers in every farm opened in August (21 farms in total).



[129] The density of soil seed banks was not assessed.

### 2.5.1. Densities of volunteers

As the study took place in late September, farmers had already started planting peanuts and most farms had already been weeded, at least partly. I still observed seedlings in every new farm I surveyed, and recorded in Mbong-Ete densities reaching up to 9.3 seedlings x $m^{-2}$ (Table 5.3). I also spotted volunteers in older farms.

**Table 5.3. Density of manioc volunteer seedlings measured in five farms**, before or after weeding. Just after the field is burned (phase 1; $K_2$), seedling densities reach up to nearly 10 seedlings x $m^{-2}$, then drop to 1 or 2 seedlings x $m^{-2}$ after the field has been weeded, just before peanuts are planted (phase 2; $A_2$, $C_1$, $I_1$, $S_1$). About a week and a half later, fields are weeded again. Seedling densities are then almost zero.

| Farms | Density/$m^2$ | Fallow length | Weeding phase |
|---|---|---|---|
| $A_2$ | 2.4 ± 6.7 | 2-3 years | 2nd |
| $C_1$ | 0.7 ± 0.6 | 3-4 years | 2nd |
| $I_1$ | 1.6 ± 2.9 | 4-7 years | 2nd |
| $K_2$ | 9.3 ± 13.2 | 4 years | 1st |
| $S_1$ | 1.3 ± 2.0 | 4 years | 2nd |
| Average | 3.0 ± 3.5 | | |

### 2.5.2. Management of manioc volunteers

All farmers in Mbong-Ete knew that manioc volunteers (**onõn-mbõng**, "birds' manioc") originate from seeds (**fis-mbõng**), and discarded them systematically. There was a general belief among farmers that unless cuttings are planted following traditional rules, they cannot give good yields. Volunteers, which grow without the intervention of farmers, produce a manioc of poor quality and should be removed as they compete with "true" manioc.

### 2.5.3. Sampling strategy

Eight landraces, three bitter and five sweet (Table 5.4), and one cohort of seedlings ($K_2$), were sampled and genotyped. Samples were collected over 17 farms. For each landrace, five samples were collected per farmer, over several farms so as to reflect the widest range of diversity within farms. The contribution of each farmer to the sample is shown in Figure 5.5.

**Table 5.4. Composition of the data set**. The table indicates the number of plants genotyped for each landrace (*N*) as well as the number of farms over which the samples were collected ($N_F$). The table also gives the frequency of the landraces amongst farmers (popularity) and their prevalence in the fields (frequency).

| | | | | **Popularity (%)** | **Frequency (%)** |
|---|---|---|---|---|---|
| **Landrace** | | ***N*** | $N_F$ | ***N = 28*** | ***N = 65*** |
| *Esobo-Nku* | Bitter | 81 | 17 | *100.0* | *100.0* |
| *Adzoro* | Bitter | 78 | 17 | *100.0* | *95.4* |
| *Nkot-Mbõng* | Bitter | 4 | 1 | *7.1* | *4.6* |
| *Akwama-Mbõng* | Sweet | 25 | 7 | *39.3* | *38.5* |
| syn. *Afouba-Mbõng* | Sweet | 33 | 7 | *32.1* | *30.8* |
| syn. *Dame Alice* | Sweet | 5 | 1 | *7.1* | *7.7* |
| syn. *Matati* a | Sweet | 15 | 3 | *17.9* | *18.5* |
| b | Sweet | 5 | 1 | *3.6* | *1.5* |
| c | Sweet | 5 | 1 | *3.6* | *1.5* |
| d | Sweet | 1 | 1 | *3.6* | *1.5* |
| *Dame Jaune* | Sweet | 3 | 2 | *7.1* | *6.2* |
| Total | | 255 | | | |

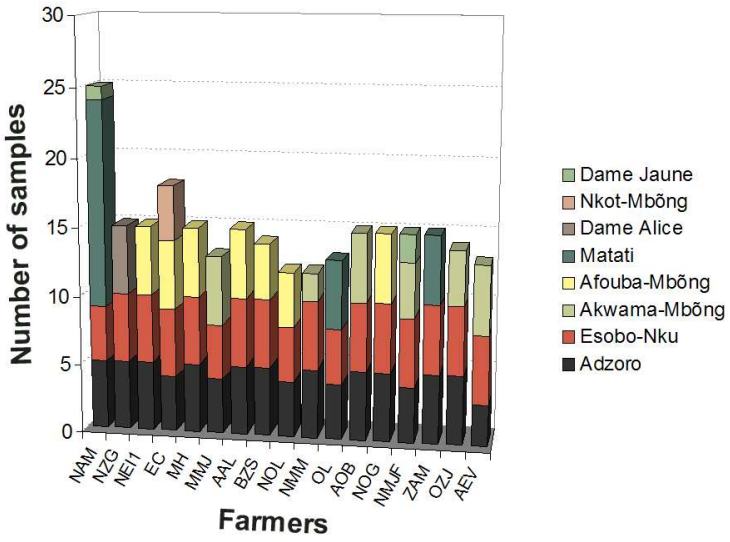



**Figure 5.5. Respective contributions of the 17 farmers to the total sample**. Because farmer NAM also distinguished sub-categories within the landrace '*Matati*', five samples were collected for each morphotype he identified.

# 3. Genetic diversity in Ntumu farms

## 3.1. Structure of genotypic diversity

Genotypic diversity consisted of 23 MLGs and 29 singletons (Table 5.5), 16 of which were found in the sole landrace '*Adzoro*' (Table 5.6). Only five MLGs consisted of more than ten plants, while thirteen groups consisted of two plants. Fifteen groups (65.2%) were specific to one landrace, and five (G3, G6, G8, G9, G10) were shared among sweet landraces, confirming that '*Afouba-Mbõng*', '*Akwama-Mbõng*', '*Dame Alice*' and '*Matati*' (morphotype a) were all synonyms and referred to the same clones. Three groups (G2, G16, G18) could not be assigned to a particular landrace.

### 3.1.1. Indexes of agreement

Farmers were highly consistent in their identifications (average index of agreement, $OA_j$, of $92\% \pm 6$, ranging from 80.7% for farmer NZG to 98.1% for farmer MMJ; 331 comparisons), and genuine assignment errors accounted for only 2.4% of the total sample.

### 3.1.2. Genotypic characterization of landraces

Landraces were genotypically well defined, with an average consistency level $C_F = 84.6\% \pm 11.7$, ranging from 66.7% ('*Dame Jaune*') to 100% ('*Matati*' *a*). The analysis of the genotypic composition of sub-landraces '*Matati*' b, c and d, however, showed that the distinction between the different morphotypes was rather loose and confused. This suggests that although farmers were aware of morphological differences, these were not sufficiently salient, and were ignored by the majority of farmers. Besides, '*Matati* a' was largely dominant in the sample (about 80% of farms surveyed). Because sweet landraces formed a monoclonal group (synonyms), I chose to group '*Afouba-Mbõng*', '*Akwama-Mbõng*' and '*Matati*' into one single category, *Akwama-Mbõng*[130], for subsequent analyses.



[130] Which is simply the generic term, in Ntumu, for "sweet manioc".

**Table 5.5a. Allelic composition of the 23 MLGs identified in Mbong-Ete** at each of the ten loci studied. The corresponding landrace is also indicated. Alleles are coded with numbers, with the numbers referring to the allele's size (in base pairs) by increasing order*.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| G1 | *Afouba-Mbõng* | 1/1 | 1/1 | 2/4 | 2/6 | 1/2 | 2/2 | 1/7 | 3/5 | 2/9 | 3/3 |
| G2 | *Akwama-Mbõng* | 1/1 | 1/1 | 4/4 | 2/6 | 2/2 | 2/2 | 1/1 | 3/3 | 2/9 | 1/3 |
| G3 | *Matati* b | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/2 | 5/7 | 3/3 | 2/6 | 2/3 |
| G4 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/3 | 1/5 | 3/3 | 2/9 | 3/3 |
| G5 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/9 | 1/3 |
| G6 | *Dame Alice* | 1/2 | 1/1 | 2/3 | 4/6 | 2/2 | 2/4 | 1/7 | 3/3 | 2/4 | 1/3 |
| G7 | *Afouba-Mbõng* | 1/2 | 1/1 | 2/3 | 1/5 | 2/2 | 2/4 | 5/7 | 3/5 | 2/6 | 2/3 |
| G8 | *Matati* a | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 2/9 | 3/3 |
| G9 | *Afouba-Mbõng* | 1/2 | 1/1 | 3/3 | 1/6 | 2/2 | 4/4 | 3/7 | 3/3 | 6/9 | 3/3 |
| G10 | *Matati* a | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/5 | 3/3 | 2/9 | 3/3 |
| G11 | *Adzoro* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/4 | 5/7 | 3/3 | 2/9 | 1/3 |
| G12 | *Adzoro* | 1/2 | 1/1 | 3/4 | 4/6 | 1/2 | 2/4 | 1/5 | 3/3 | 2/2 | 1/3 |
| G13 | *Adzoro* | 1/2 | 1/1 | 3/4 | 1/6 | 1/2 | 2/3 | 1/3 | 3/3 | 6/9 | 1/3 |
| G14 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/3 | 5/7 | 1/3 | 6/9 | 2/3 |
| G15 | *Esobo-Nku* | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/3 | 5/7 | 3/6 | 4/9 | 2/3 |
| G16 | *Matati* c | 1/2 | 1/1 | 3/4 | 2/4 | 1/1 | 2/3 | 3/7 | 3/6 | 4/9 | 2/3 |
| G17 | *Matati* b | 1/2 | 1/1 | 3/4 | 2/4 | 1/2 | 2/3 | 3/7 | 3/6 | 4/9 | 2/3 |
| G18 | *Esobo-Nku* | 1/2 | 1/1 | 3/4 | 3/6 | 2/2 | 2/2 | 1/1 | 3/6 | 5/9 | 1/2 |
| G19 | *Dame Jaune* | 2/2 | 1/1 | 3/3 | 1/2 | 2/3 | 2/3 | 1/2 | 4/5 | 5/9 | 3/3 |
| G20 | *Matati* c | 2/2 | 1/1 | 2/3 | 1/6 | 1/1 | 2/4 | 3/3 | 3/3 | 6/9 | 3/3 |
| G21 | *Esobo-Nku* | 2/2 | 1/1 | 2/3 | 1/6 | 1/1 | 2/4 | 3/7 | 3/3 | 6/9 | 3/3 |
| G22 | *Esobo-Nku* | 2/2 | 1/1 | 2/3 | 1/6 | 1/2 | 2/4 | 3/7 | 3/3 | 6/9 | 3/3 |
| G23 | *Esobo-Nku* | 2/2 | 1/1 | 2/3 | 6/6 | 1/2 | 2/4 | 3/7 | 3/3 | 6/9 | 3/3 |

* Corresponding sizes are given in Appendix C3.

**Table 5.5b. Allelic composition of the 29 singletons identified in Mbong-Ete**.

| MLG | Landrace | Allelic composition at SSR loci | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | GAGG5 | GA21 | GA57 | GA126 | GA134 | GA12 | SSR31 | SSR55 | SSR68 | SSR169 |
| 1 | *Adzoro* | 1/2 | 1/1 | 3/4 | 1/6 | 1/2 | 2/3 | 5/7 | 1/3 | 6/9 | 2/3 |
| 2 | *Adzoro* | 2/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/9 | 1/3 |
| 3 | *Adzoro* | 1/2 | 1/1 | 2/3 | 6/6 | 2/2 | 3/4 | 5/7 | 3/3 | 9/9 | 3/3 |
| 4 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/2 | 1/3 |
| 5 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/4 | 5/7 | 3/3 | 2/9 | 1/3 |
| 6 | *Adzoro* | 1/2 | 1/1 | 2/2 | 1/3 | 2/2 | 2/2 | 7/7 | 3/5 | 2/9 | 3/3 |
| 7 | *Adzoro* | 1/2 | 1/1 | 2/2 | 6/6 | 2/2 | 2/4 | 7/7 | 3/3 | 9/9 | 3/3 |
| 8 | *Adzoro* | 1/2 | 1/1 | 1/3 | 3/6 | 2/2 | 2/4 | 5/7 | 3/3 | 2/9 | 1/3 |
| 9 | *Adzoro* | 1/2 | 1/1 | 2/2 | 6/6 | 2/2 | 2/3 | 5/7 | 1/3 | 6/9 | 2/3 |
| 10 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 4/4 | 3/7 | 3/3 | 6/9 | 3/3 |
| 11 | *Adzoro* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 5/7 | 5/5 | 2/6 | 2/3 |
| 12 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/3 | 5/7 | 5/5 | 2/6 | 2/3 |
| 13 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 5/7 | 1/3 | 6/9 | 2/3 |
| 14 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 2/2 | 2/3 | 5/7 | 1/3 | 6/9 | 2/3 |
| 15 | *Adzoro* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/3 | 5/7 | 1/3 | 6/6 | 2/3 |
| 16 | *Adzoro* | 2/2 | 1/1 | 2/3 | 1/6 | 1/2 | 4/4 | 3/7 | 3/3 | 6/9 | 3/3 |
| 17 | *Afouba-Mbõng* | 1/1 | 1/1 | 2/4 | 2/6 | 1/2 | 2/2 | 5/7 | 3/3 | 2/6 | 2/3 |
| 18 | *Afouba-Mbõng* | 1/2 | 1/1 | 3/4 | 2/3 | 2/2 | 2/3 | 1/2 | 3/5 | 5/9 | 3/3 |
| 19 | *Afouba-Mbõng* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/2 | 5/7 | 3/3 | 2/6 | 2/3 |
| 20 | *Afouba-Mbõng* | 1/2 | 1/1 | 2/3 | 4/6 | 1/2 | 2/2 | 3/7 | 3/6 | 4/9 | 2/3 |
| 21 | *Akwama-Mbõng* | 1/2 | 1/1 | 2/3 | 6/6 | 1/2 | 2/4 | 4/5 | 2/3 | 5/5 | 2/3 |
| 22 | *Akwama-Mbõng* | 1/1 | 1/1 | 4/4 | 6/6 | 2/2 | 2/2 | 1/1 | 3/3 | 2/9 | 1/3 |
| 23 | *Dame Alice* | 1/2 | 1/1 | 2/3 | 3/5 | 2/2 | 2/3 | 5/7 | 5/5 | 2/6 | 2/3 |
| 24 | *Esobo-Nku* | 1/2 | 1/1 | 3/4 | 1/6 | 2/2 | 2/2 | 1/1 | 3/6 | 5/9 | 1/2 |
| 25 | *Esobo-Nku* | 2/2 | 1/1 | 2/3 | 6/6 | 1/1 | 2/2 | 3/7 | 3/3 | 9/9 | 3/3 |
| 26 | *Esobo-Nku* | 2/2 | 1/1 | 3/3 | 1/6 | 2/2 | 2/4 | 3/3 | 3/3 | 6/9 | 3/3 |
| 27 | *Esobo-Nku* | 1/2 | 1/1 | 2/3 | 3/6 | 1/2 | 2/4 | 1/1 | 3/6 | 6/9 | 1/2 |
| 28 | *Esobo-Nku* | 1/2 | 1/1 | 3/3 | 1/6 | 1/1 | 2/2 | 3/7 | 1/3 | 6/9 | 2/3 |
| 29 | *Matati* c | 2/2 | 1/1 | 2/3 | 1/6 | 1/2 | 2/4 | 3/3 | 3/3 | 6/9 | 3/3 |

**Table 5.6. Genotypic composition of landraces in Mbong-Ete**. Genotypes were grouped into 'typical', 'non-typical' and 'atypical' categories, according to their distribution amongst landraces. Typical genotypes were either 'specific' when restricted to one landrace, or 'shared' in the case of synonymies. Number of individuals is indicated between brackets. Consistency of identifications amongst farmers ($C_F$) is also given for each landrace, except those that were sampled only over one farm. Plants that show a genotype typical of another landrace than the one farmers assigned them to were reported in the 'mistaken' column.

| Landraces | | | *N* | Typical | | Non-typical | Atypical | Mistaken | $C_F$ (%) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Specific | Shared | | | | |
| *Esobo-Nku* | | Bitter | 81 | G15 (3), G21 (5), G22 (60), G23 (2) | — | G18 (6) | 5 | — | *93.8* |
| *Adzoro* | | Bitter | 78 | G4 (2), G5 (24), G11 (2), G12 (2), G13 (2), G14 (29) | — | — | 16 | G10 (1) | *78.2* |
| *Nkot-Mbõng* | | Bitter | 4 | — | — | G18 (4) | — | — | — |
| *Akwama-Mbõng* | | Sweet | 25 | — | G6 (2), G8 (1), G9 (1), G10 (13) | G2 (1), G18 (3) | 2 | G5 (1), G15 (1) | *84.0* |
| syn. *Afouba-Mbõng* | | Sweet | 33 | G1 (3), G7 (2) | G3 (3), G6 (1), G9 (1), G10 (18) | — | 4 | G21 (1) | *84.8* |
| syn. *Dame Alice* | | Sweet | 5 | — | G6 (2), G10 (2) | — | 1 | — | — |
| syn. *Matati* | a | Sweet | 15 | — | G6 (2), G8 (1), G10 (12) | — | — | — | *100.0* |
| | b | Sweet | 5 | G17 (2) | G3 (2) | G16 (1) | — | — | — |
| | c | Sweet | 5 | G20 (2) | — | G16 (1) | 1 | G14 (1) | — |
| | d | Sweet | 1 | — | — | G2 (1) | — | — | — |
| *Dame Jaune* | | Sweet | 3 | G19 (2) | — | — | — | G22 (1) | *66.7* |

Unlike the two other landraces, which consisted of one largely dominant clone and several minor MLGs (Figures 5.6a,b,c), '*Adzoro*' was composed of two major clones G5 and G14, and encompassed a large proportion of plants with atypical genotypes (Figure 5.6c).

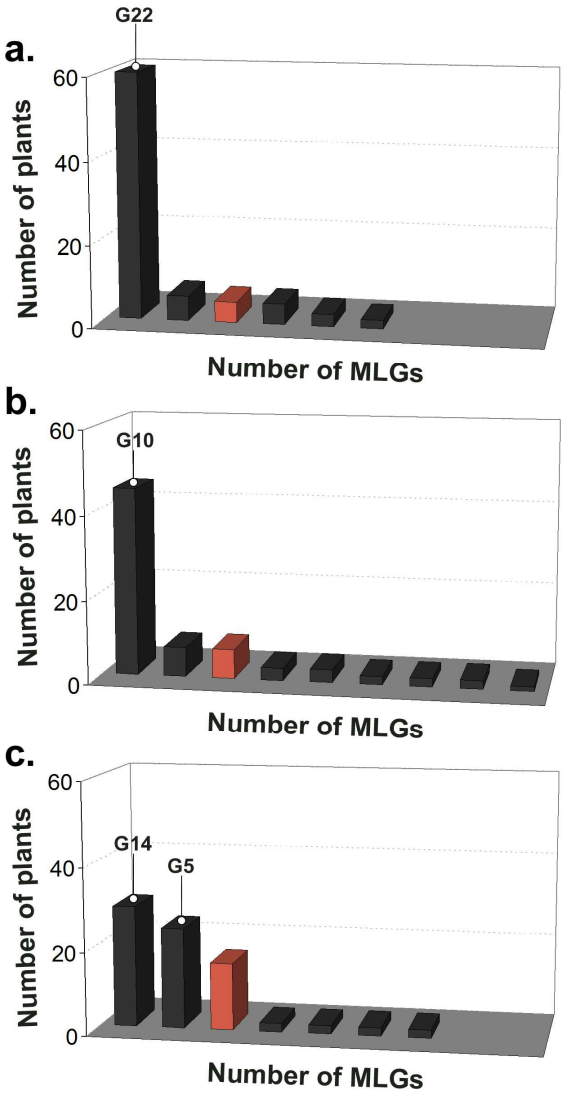



**Figure 5.6. Genotypic composition of the three main Ntumu landraces**, (a) '*Esobo-Nku*' ($N = 81$), (b) *Akwama-Mbõng* ($N = 75$), and (c) '*Adzoro*' ($N = 77$). Atypical genotypes (red bars) were grouped as a single category. Atypical genotypes represented 6.2%, 9.6% and 22.2% of the total plants sampled for '*Esobo-Nku*', *Akwama-Mbõng*, and '*Adzoro*', respectively.

### 3.1.3. Distribution of MLGs among farmers

Examining in greater detail the distribution among farmers of the different MLGs composing the landrace '*Adzoro*', one can see that the two main clones, G5 and G14, were not homogeneously distributed among farmers. With only one exception (NZG), farmers grew either G5 or G14, but never a mixture of the two clones (Figure 5.7).

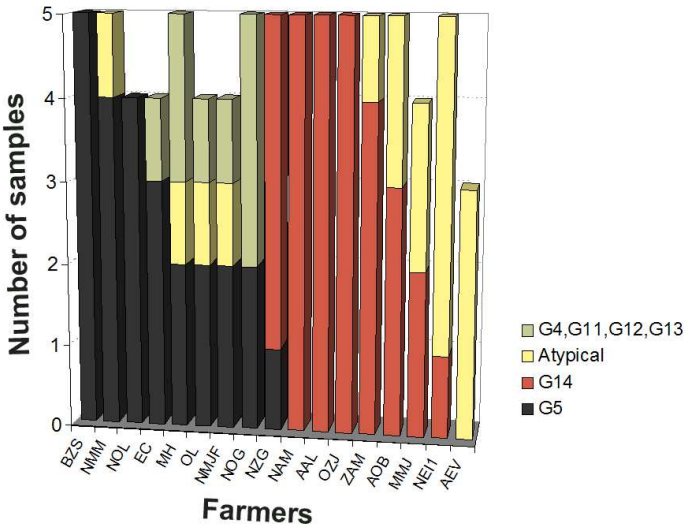



**Figure 5.7. Distribution among farmers[131] of the MLGs composing the landrace '*Adzoro*'**. Minor MLGs (G4, G11, G12, and G13, each of which accounts only for a few plants) were grouped in a single category.

It was possible to draw a parallel between the distribution of G5 and G14 among farmers and farmers' kin relationships (Figure 5.8). The two genotypes formed several groups of genotypic uniformity, which all corresponded to affinal chains of transmission (mother-in-law to daughter-in-law), independent of the eight family nuclei.



[131] Farmers are referred to by their initials.

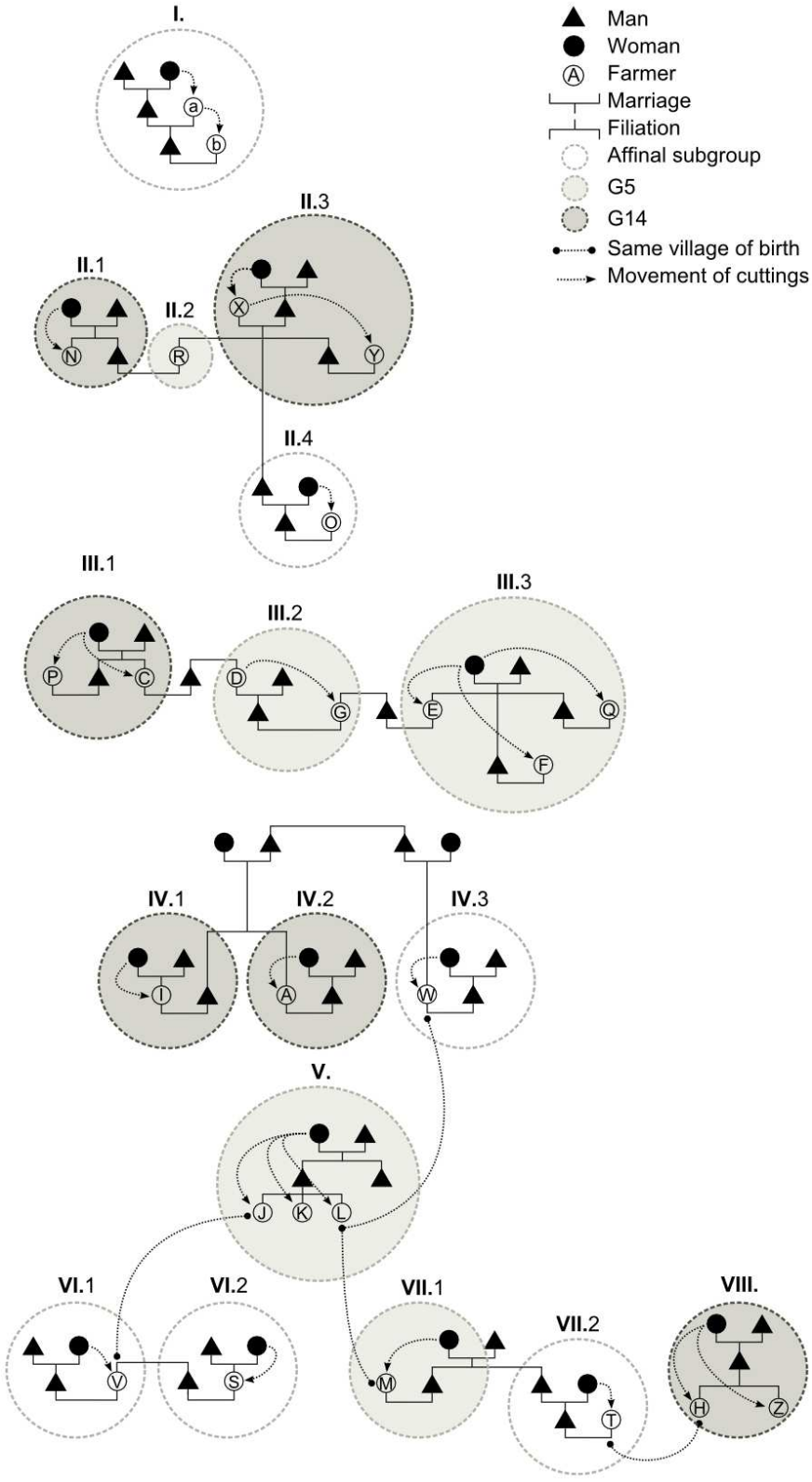



**Figure 5.8. Farmers' kinship networks in Mbong-Ete**. Eight family nuclei (numbered I to VIII) could be identified. Affinal subgroups, which correspond to groups of farmers linked to the same source of cuttings, were also identified within the nuclei. For clarity, farmers were attributed letters in chronological order of interview: A : NAM, B : NZG, C : $NEI_1$, D : EM, E : NMC, F : EC, G : MH, H : MMJ, I : AAL, J : BZS, K : NOL, L : NMM, M : OL, N : ZOB, O : OOI, P : ZE, Q : BP, R : NOG, S : EOJ, T : AJ, U : NMJF, V : AMT, W : ONJ , X : ZAM, Y : OZJ, Z : AEV, b : $NEI_2$, a : MET. No information was available for farmer B and farmer U.

## 3.2. Allelic diversity

Allelic diversity in Mbong-Ete ($\hat{A} = 3.9 \pm 0.1$) was significantly lower (one-way ANOVA followed by Tukey's *post-hoc* test, $F = 375.4$, df = 5, $P < 10^{-4}$) than in the other villages studied (Figure 5.9).

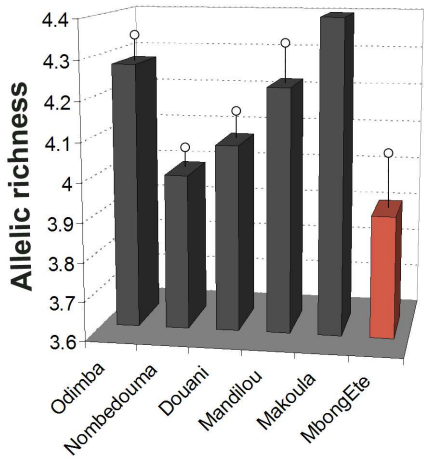



**Figure 5.9. Comparison of allelic diversity ($\hat{A}$) across six villages**, averaged over the 10 loci. Standard deviation (bullets) is also given. Allelic richness was estimated after removal of clonal replicates and standardization to a common sample size of 45 MLGs, using the multiple random reduction method proposed by Leberg (2002).

Allelic frequencies for the ten loci studied are shown for the three landraces in Figure 5.10. I found five[132] rare alleles (frequency < 1%), four of which I found in only one single copy in the whole sample. One ($GA57_{156}$) was private to '*Adzoro*', and the three others ($SSR31_{168,181}$, and $SSR55_{129}$) were private to *Akwama-Mbõng*[133].

$SSR31_{178}$ was more frequent in '*Esobo-Nku*' than in the other two landraces. Several alleles, frequent among other landraces, were either missing in '*Esobo-Nku*' ($GA21_{110}$, $SSR55_{141}$, $SSR68_{250}$), or found in very low frequency ($GAGG5_{114}$, $GA126_{191}$, $GA12_{146}$, $SSR31_{183}$). One allele, $GA21_{112}$, was fixed in the population, and several other alleles ($GAGG5_{123}$, $SSR55_{133}$, $SSR169_{101}$) were found almost only at the homozygous state in '*Esobo-Nku*'. Likewise, for all the loci studied[134], levels of polymorphism (*PIC*) were generally lower for '*Esobo-Nku*' than for '*Adzoro*' and *Akwama-Mbõng* (Figures 5.11a,b).

[132] In fact, I also detected $GA134_{325}$, but only in two of the three plants I collected for the landrace '*Dame Jaune*', and which I did not include in the analyses.

[133] $SSR31_{168}$ was also detected in '*Dame Jaune*'.

[134] Except for GA134, which showed higher *PIC* in '*Esobo-Nku*'.

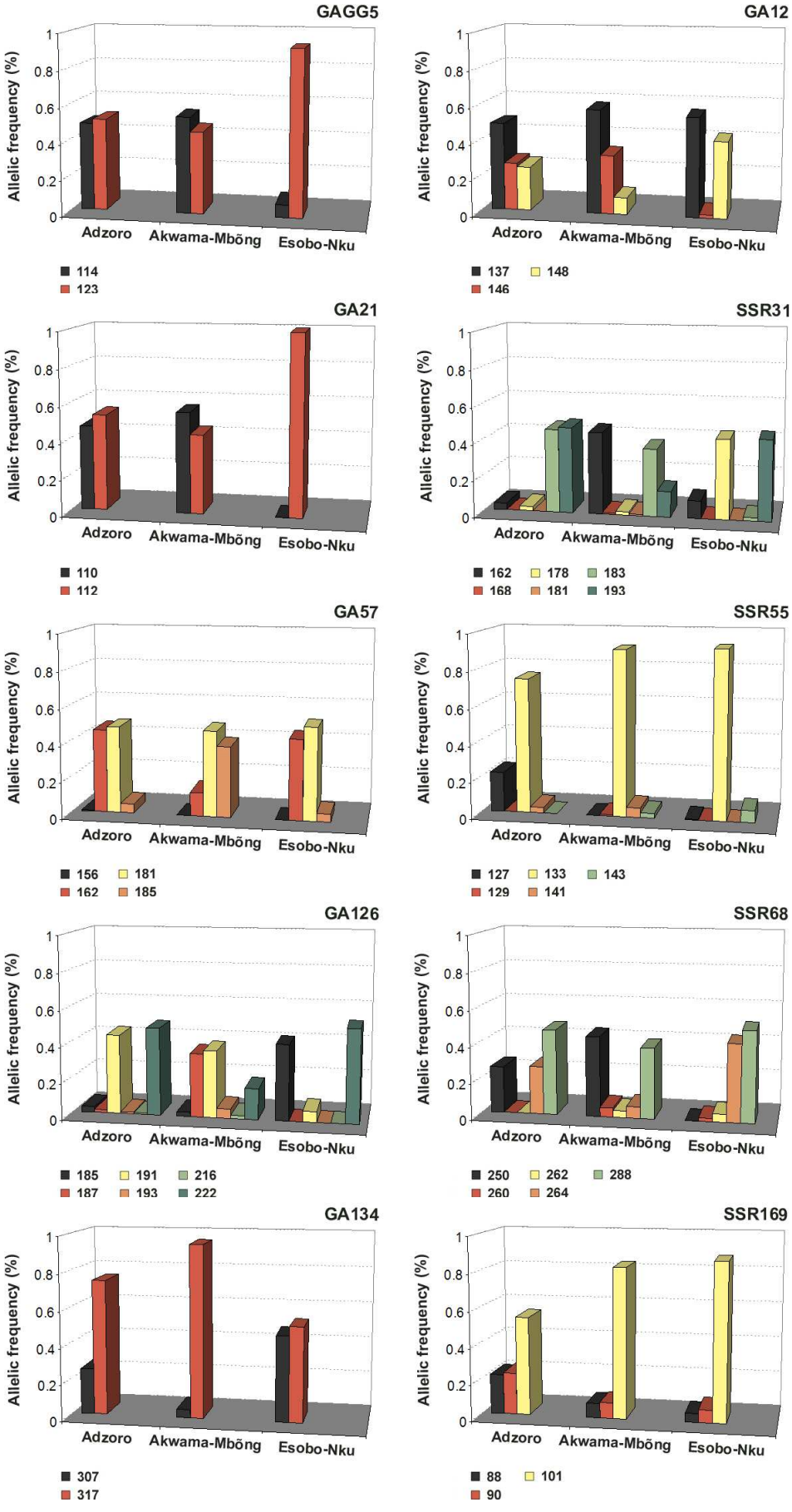



**Figure 5.10. Comparison of allelic frequencies in the three Ntumu landraces.**

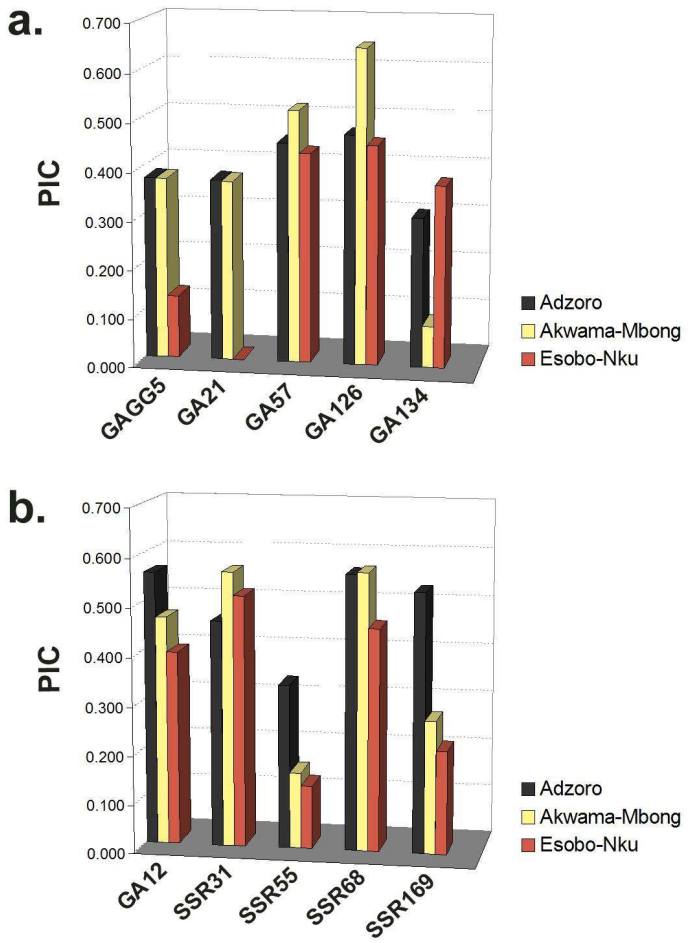



**Figure 5.11. Levels of polymorphism (*PIC*)** calculated for each of the ten loci scored in the three Ntumu landraces, '*Adzoro*', *Akwama-Mbõng* and '*Esobo-Nku*'.

Allelic composition also varied greatly between the two main genotypes of '*Adzoro*', G5 and G14 (Table 5.5). Table 5.7 shows the values of pairwise differentiation between the three main Fang landraces ($N_C \geq 10$). All pairs of varieties were highly and significantly differentiated, with the lowest genetic differentiation between '*Adzoro*' and '*Akwama-Mbõng*' ($F_{ST} = 0.101$, $P < 0.01$). On the neighbour-joining tree presented in Appendix C3, '*Adzoro*' grouped together with sweet landraces. There was also a strong genetic differentiation between the two main genotypes of '*Adzoro*' ($F_{ST} = 0.357$). G5 showed lower genetic differentiation with '*Akwama-Mbõng*' (sweet, $F_{ST} = 0.174$) than with '*Esobo-Nku*' (bitter, $F_{ST} = 0.375$), whereas G14 did not show any significant difference.

**Table 5.7. Pairwise genetic differentiation ($F_{ST}$) between the Fang landraces** (upper-right matrix), with '*Adzoro*' treated as a whole and as two independent genotypic groups (G5 and G14), and their significance level (lower-left matrix). Only landraces for which $N_C \geq 10$ were considered. '*Nkot-Mbõng*' ($N = 4$) and '*Dame Jaune*' ($N = 3$) were excluded.

| | *Adzoro* | *Adzoro* G5 | *Adzoro* G14 | *Akwama-Mbõng* | *Esobo-Nku* |
|---|---|---|---|---|---|
| *Adzoro* | | — | — | 0.101 | 0.178 |
| *Adzoro* G5 | — | | 0.357 | 0.174 | 0.375 |
| *Adzoro* G14 | — | ** | | 0.249 | 0.230 |
| *Akwama-Mbõng* | ** | ** | ** | | 0.276 |
| *Esobo-Nku* | ** | ** | ** | ** | |

** *P*-value < 0.01 (Benjamini & Hochberg's sharpened test). "—" indicates that the test was not performed.

No genetic differentiation was found between the different constituents of the *Akwama-Mbõng* cluster (Table 5.8), however there was significant differentiation between the different morphotypes of '*Matati*'.

**Table 5.8. Pairwise genetic differentiation ($F_{ST}$) between sweet maniocs**. $N_C \geq 5$ only. '*Matati*' d, for which only one individual was sampled, was excluded.

| | *Afouba-Mbõng* | *Akwama-Mbõng* | *Dame Alice* | *Matati* a | *Matati* b | *Matati* c |
|---|---|---|---|---|---|---|
| *Afouba-Mbõng* | | 0.011 | 0.009 | 0.015 | 0.078 | 0.228 |
| *Akwama-Mbõng* | *NS* | | 0.026 | 0.014 | 0.097 | 0.245 |
| *Dame Alice* | *NS* | *NS* | | 0.050 | 0.066 | 0.265 |
| *Matati* a | *NS* | *NS* | *NS* | | 0.169 | 0.335 |
| *Matati* b | *NS* | * | *NS* | ** | | 0.100 |
| *Matati* c | ** | ** | * | ** | *NS* | |

** *P*-value < 0.01, * *P*-value < 0.05, *NS* not significant.

Of the total genetic diversity found in Mbong-Ete (average over the loci, $F_{IT} = -0.213 \pm 0.083$, $P < 0.01$), the between-landraces component was the highest ($F_{ST} = 0.188 \pm 0.027$, $P < 0.01$), while the contribution of within-landrace diversity was moderate ($F_{IS} = -0.494 \pm 0.073$, $P < 0.01$).

## 3.3. Overview of genetic diversity in Mbong-Ete

Gene diversity ($H_E$), private alleles and other diversity indexes computed for each landrace are summarized in Table 5.9. All three landraces showed negative values of $F_{IS}$, indicative of a strong heterozygote excess, and on average, low values of clonal richness ($R = 0.197 \pm 0.008$). Genotypic diversity and allelic richness were lower for '*Esobo-Nku*' than for the other two landraces.

**Table 5.9. Diversity statistics computed for each landrace**, after correction for assignment errors (*Nc*). The table shows the number of distinct genotypes in each landrace (*G*), observed ($H_O$) and expected ($H_E$) heterozygosity, $F_{IS}$, allelic richness ($A_R$, averaged over the loci), private alleles ($A_p$), and an index of clonal richness (*R*). Only landraces for which $N_C \geq 10$ were considered[135]. Synonyms ('*Akwama-Mbõng*', '*Afouba-Mbõng*', '*Matati* a', '*Dame Alice*') were all grouped under the same category, *Akwama-Mbõng*.

| Landrace | $N_C$ | $G$ | $H_O$ | $H_E$ | $F_{IS}$ | $A_R$ | $A_p$ | $R$ |
|---|---|---|---|---|---|---|---|---|
| *Esobo-Nku* | 81 | 10 | 0.593 | 0.375 | -0.575* | 2.8 | — | 0.113 |
| *Adzoro* | 77 | 22 | 0.778 | 0.532 | -0.458* | 3.2 | $GA57_{156}$ | 0.276 |
| *Akwama-Mbõng* | 75 | 16 | 0.677 | 0.466 | -0.449* | 3.6 | $SSR31_{168}$ $SSR31_{181}$ $SSR55_{129}$ | 0.203 |

* *P*-value < 0.001.

## 3.4. Genetic diversity of seedlings

Volunteer seedlings collected in farm $K_2$ were partly issued from selfing (estimated rate of selfing, $s = 0.199$; CI95[136] = [0.043,0.336]). Several alleles detected in landraces were missing among seedlings ($GA57_{156}$, $GA126_{193,216}$, $SSR31_{168,181}$, $SSR55_{129,141,143}$, and $SSR68_{260,262}$).

A parent-offspring analysis, using the typical MLGs of each landrace as potential parents, showed that most seedlings (21/31) could be offspring of the landrace '*Adzoro*' (G5, G14), and only 7/31 and 3/31 could be offspring of '*Esobo-Nku*' (G22) and *Akwama-Mbõng* (G10), respectively (Table 5.10). Also, while 20 seedlings could be offspring of G5, only one could be offspring of G14.



[135] '*Dame Jaune*', and '*Matati* b', 'c', and 'd', were omitted.

[136] Confidence interval 95%.

**Table 5.10. Parent-offspring analysis of the 31 seedlings collected in $K_2$**, using the likelihood method. Only the five most common typical MLGs (G5, G10, G14, G18 and G22) were considered as potential 'mothers'. Only the best LOD score for each seedling is given. LOD critical values (2.70 and 1.06, for $P < 0.01$ and $P < 0.05$, respectively) were estimated after 100,000 iterations. Where no *P*-value is associated to the LOD score, no potential 'mother' with a *P*-value below the specified significance levels could be assigned to the seedling. Wherever no potential mother could be found, the MLG column was left blank.

| Volunteers | MLG | LOD | *P*-value |
|---|---|---|---|
| $K_2$-05 | G5 | 4.89 | *< 0.01* |
| $K_2$-31 | G5 | 4.39 | *< 0.01* |
| $K_2$-09 | G5 | 4.23 | *< 0.01* |
| $K_2$-28 | G5 | 4.17 | *< 0.01* |
| $K_2$-14 | G5 | 3.85 | *< 0.01* |
| $K_2$-20 | G5 | 3.70 | *< 0.01* |
| $K_2$-25 | G5 | 3.60 | *< 0.01* |
| $K_2$-27 | G5 | 3.48 | *< 0.01* |
| $K_2$-01 | G5 | 3.46 | *< 0.01* |
| $K_2$-23 | G5 | 3.38 | *< 0.05* |
| $K_2$-16 | G5 | 3.08 | *< 0.01* |
| $K_2$-21 | G5 | 2.90 | *< 0.01* |
| $K_2$-11 | G5 | 2.61 | *< 0.05* |
| $K_2$-10 | G5 | 2.51 | |
| $K_2$-18 | G5 | 2.49 | |
| $K_2$-04 | G5 | 2.26 | *< 0.05* |
| $K_2$-26 | G5 | 1.73 | |
| $K_2$-15 | G5 | 1.39 | *< 0.05* |
| $K_2$-24 | G5 | 1.23 | *< 0.05* |
| $K_2$-08 | G5 | 1.22 | |
| $K_2$-19 | G22 | 3.14 | *< 0.01* |
| $K_2$-29 | G22 | 3.13 | *< 0.01* |
| $K_2$-06 | G22 | 2.70 | *< 0.05* |
| $K_2$-17 | G22 | 1.27 | |
| $K_2$-22 | G22 | 1.26 | *< 0.05* |
| $K_2$-12 | G22 | $7.39 \times 10^{-1}$ | |
| $K_2$-03 | | -3.58 | |
| $K_2$-13 | G14 | 3.51 | *< 0.01* |
| $K_2$-02 | G10 | 3.97 | *< 0.05* |
| $K_2$-30 | G10 | 1.41 | *< 0.05* |
| $K_2$-07 | G10 | $5.09 \times 10^{-1}$ | |

# 4. Three borders, three landraces

With only three[137] landraces, the level of named diversity in Mbong-Ete was the lowest I recorded in Gabon. The Ntumu showed very little interest in growing many manioc landraces[138], a striking difference with most manioc farmers in Gabon (*e.g.*, the Myènè [B.11], the Tsogho [B.31], and the Ghisir [B.41] in the previous chapters[139]) and around the world, *e.g.*, the *Caiçara* in Brazil (Sambatti *et al.* 2001), the Makushi in Guyana (Elias *et al.* 2000a), the Tukano in Colombia (Dufour & Wilson 1996, Chernela 1987), or the Aguaruna (Boster 1984b) and the Amuesha (Salick *et al.* 1997) in Peru. Even the very popular '*Dame Jaune*', which I recorded in almost every other village I surveyed[140], did not meet a great success amongst Ntumu farmers.

In the rest of Gabon, the number of landraces per village averaged 30[141]. Why, given the considerable diversity available at the country scale, is varietal diversity so low in Mbong-Ete and northern Gabon? Answering this question requires contemplating again the history of manioc agriculture in the Woleu-Ntem province, and pondering about the historical and cultural factors that durably shaped manioc varietal diversity in northern Gabon.

## 4.1. The colonial legacy

Far from being the exception, a low number of landraces seemed constant across northern Gabon. I found the same set of three landraces ('*Adzoro*', '*Esobo-Nku*', *Akwama-Mbõng*) in Bitam, and they seemed common to most of the Woleu-Ntem, including the bordering regions in Cameroon and Equatorial Guinea from where some of my informants originated.

[137] In fact five, counting '*Dame Jaune*' and '*Nkot-Mbõng*', but those were relatively trivial.

[138] That is, they did not see any point in expanding their range of manioc landraces, having already three that fulfil their requirements. However, they do not disregard diversity in their farms, and do maintain several types of yams, plantains and bananas.

[139] See also Delêtre (2004).

[140] See Appendix B4.

[141] Average computed over 13 villages (including data from Binot 1998 and Soengas 2010).

I have highlighted in introduction the extent to which colonial administrations encouraged manioc cultivation in northern Gabon and southern Cameroon. Promoting manioc obeyed both a political and an economic rationale: securing food for populations in the short term, while, in the long term, transforming the regional agriculture into cash-cropping with the development of cacao plantations (Sautter 1966, Guyer 1978, Dounias 1993). Yet, by interfering in local farming and promoting a probably limited range of varieties, the colonial authorities also favoured regional homogeneity.

Sweet manioc perhaps best exemplifies this durable imprint of colonial agricultural policies on manioc regional diversity. During the German occupation of Cameroon (1884-1916), sweet manioc varieties from the West Indies were introduced into French Equatorial Africa, and successfully spread up throughout the region (Mouton 1949, Jones 1959). A comparison of the landraces recorded in Mbong-Ete and those listed by Angladette (1949) in Cameroon suggests that manioc diffused into northern Gabon from Cameroon, corroborating the historical trajectory of manioc proposed by Rossel (1987). Together with 16 other manioc landraces, Angladette mentions '*Afobo*' (apparently originating from Yaoundé) and '*Adzoro-Mbõng*' as two of the most common manioc landraces grown in Cameroon, strongly suggesting manioc diffused into northern Gabon from Cameroon. Amid the landraces he found among the Mvae and the Yasa[142], in south-western Cameroon, Dounias (1993) also mentions '*Afobo*' and '*Adzobo*' ("the early"), a bitter cultivar phonetically close to '*Adzoro*'.

Between 1904 and 1909, Tessmann (1913) studied Fang communities in south-western Cameroon and in the north of Equatorial Guinea, and mentioned only seven manioc landraces for the whole area. Almost a century later, Dounias (1993) visited nine communities[143] in the same area, and recorded in total 26 distinct names, but the average number of landraces per village was only seven.

The comparison of the study by Tessmann in 1913 among the Fang (Mvae [A.75f] and Ntumu [A.75a] in south Cameroon and north Equatorial Guinea), and that of Dounias (1993), suggests that the initial apport of manioc varietal diversity in the region was quite limited, and that it is the colonial administration that put in place the limited range of varietal diversity which is now found in the Woleu-Ntem.



[142] The Yasa belong to the Bubi-Benga group [A.30] (Guthrie 1948, Maho 2003).

[143] Mvae principally (although 85% of the population in the region is Ntumu).

## 4.2. Many names, one same clone

Obviously, Fang landraces are not circumscribed to the Woleu-Ntem. In Mbong-Ete, farmers had up to four different names for sweet manioc (‘*Afouba-Mbõng*’, ‘*Akwama-Mbõng*’, ‘*Dame Alice*’ and ‘*Matati*’), all of which were synonymous[144], and corresponded to one largely dominant clone, G10. The neighbour-joining analysis presented in Appendix C3 shows that G10 is actually a clonemate of the landrace ‘*Ngõndoyem*’ (“the lady from Oyem”), which I had previously recorded in Douani near Sindara (Ngounié), and of ‘*Gõndoyem*’, which I found in Imbong, near Mékambo (Ogooué-Ivindo). The same landrace (‘*Ngõngeoyem*’) was also reported ten years ago around La Lopé[145] (Binot 1998). But while manioc landraces readily diffuse outside the Fang realm, no exchanges seem to take place in the other direction. Hence, if the narrow range of named diversity at the regional scale has originally historical causes, cultural factors must have kept the Woleu-Ntem relatively isolated from the rest of the country, and contributed to maintaining low levels of manioc diversity at the regional scale.

## 4.3. A closed system

Just as mingling of cultures promotes human diversity, it also promotes crop diversity (Harlan 1975). Yet, in sharp contrast with all other provinces in Gabon, the Woleu-Ntem is striking by its ethnic homogeneity. About 99% of the population of northern Gabon is Fang (Joiris & Bahuchet 1994), while everywhere else in the country populations are mixed (Perrois *et al.* 1983), a diversity which is even found down to the village level[146].

In many communities, women, through marriages, are the main vectors of the diffusion of manioc landraces, and by exchanging wives, villages also exchange landraces (Chernela 1987, Emperaire & Peroni 2007). Manioc diversity can thus be increased, or at least maintained, through the mobility and exchangeability of genotypes between farmers and villages, helped in this respect by movements of people. In fact, the Ntumu kinship system precludes the introduction of exogenous planting material.



[144] Consistently, when listing all the landraces they grew, farmers never used more than one name for sweet manioc. However, they were aware of the synonymy between the different appellations used in the village.

[145] Among the Fang Makina, but not among neighbouring communities (Okande, Simba, Sake).

[146] See for example Mopia in the Haut-Ogooué (mixed community of Kaningi, Ndassa, Teke, Wumbu, Mbanwe, Kota, Mbamba), Odimba in the Ogooué-Maritime (Orungu, Punu, Nkomi, Kèlè), Imbong in the Ogooué-Ivindo (Koya, Kwele, Mwessa), or Douani in the Ngounié (Tsogho, Ghisir, Eviya).

The Ntumu are patrilinear and virilocal, and to comply with their strict exogamy rules[147], Ntumu must seek wives outside the village. It is the tradition that, when she marries, the young wife moves empty-handed to her husband's village (Carrière 1999). There, she receives from her mother-in-law all she needs to start her own plantations. Such affinal transmission was the rule in Mbong-Ete, and 75% of the farmers I interviewed had received their manioc cuttings from their mother-in-law[148]. In essence, this means that the Ntumu kinship system maintains low varietal diversity, hereby also low genotypic diversity, at the village level.

### 4.3.1. Clones and clans

Two common genotypes of '*Adzoro*', G5 and G14, coexist in Mbong-Ete. Each accounted for nearly half the plants sampled, and one was grown by some farmers, but not by others who only grew the other one. Such a clear division between farmers suggests that little material is exchanged at the village level.

Exchanging cuttings is a common practice among manioc farmers. In communities growing a large diversity of landraces, exchanges of cuttings are frequent (Boster 1985b, 1986, Chernela 1987, Emperaire *et al.* 1998, Peroni 1998, Elias *et al.* 2000a, Sambatti *et al.* 2001). Farmers seek new landraces to try, and when spotting an interesting morphotype in a neighbour's garden, ask for a few cuttings to experiment with the new landrace. In Mbong-Ete, varietal diversity is very low. Farmers all grow the same landraces and have no need to ask their neighbours for cuttings. Farmers lack the main grounds that would make exchange of planting material of interest, namely, *diversity*. Varietal uniformity at the village level thus hampers horizontal transfers of planting material, preventing the homogenization of genotypic diversity among families, while the kinship system maintains a clear partitioning of genotypic diversity along affinal chains.

As a result of virilocality, Fang villages are usually monoclanic (Murdock 1959, Dounias 1993). Men all belong to the same clan (**ayõng**), and form an integrated kin group (Murdock 1959). This organisational scheme is constant all over the Fang realm,



[147] Under the traditional Fang kinship rules, membership of the clan is inherited from the father ("agnatic lineage", Laburthe-Tolra 1981). In this system, also called "nested lineage" (Balandier 1982), an individual belongs not only to his father's clan but also those of his forefathers. The rule of strict clanic exogamy forbids marriages between a man and a woman belonging to the same clan, and applies at least to the last five generations (Cadet 2009).

[148] The other 25% were farmers born in the village.

and the only known exceptions are the result of the arbitrary grouping of villages ordered by the colonial administration (Dounias 1993, Knight 2003). Although the clanic organisation of Mbong-Ete was not specifically studied[149], the co-existence of two major clones (G5 and G14) for '*Adzoro*', their strong genetic differentiation and their distribution pattern among farmers, suggests that Mbong-Ete arose from two patrilineages of different origins, that merged following the relocation of Mimbang-Alèn and the creation of Mbong-Ete, each bringing along a different clone of '*Adzoro*'[150].

## 4.4. Or many clones and one single name?

The study of transfer of cuttings in Mbong-Ete highlights an important point: that people, not landraces, move within the Fang realm. Mbong-Ete behaves like a closed system. No new landrace is incorporated into the varietal pool, while embedded landraces are kept isolated from the rest of the country's manioc gene pool. In such conditions, both genotypic and allelic diversity are expected to decrease gradually with each cropping season (Figure 5.12).

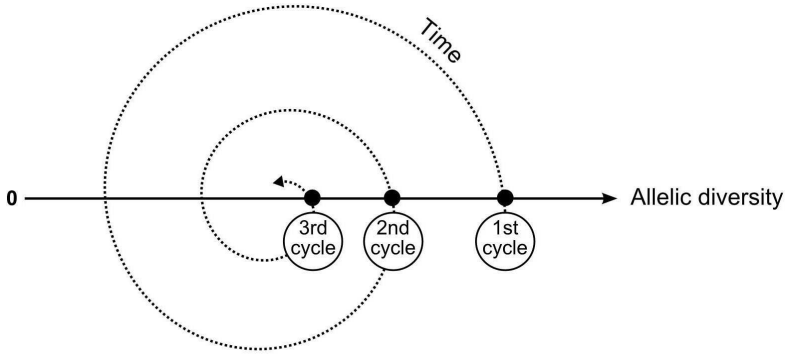



**Figure 5.12. Theoretical evolution of allelic diversity in a closed system**. Each time farmers start a new cropping season, some allelic diversity is lost, as only a small proportion (between 10 and 15%, Elias 2000) of individuals is propagated. At the level of the village, this results in an overall reduction of allelic and genotypic diversity. At the level of the landrace, it eventually results in all landraces being monoclonal.

[149] The majority of farmers being women, knowing their clan does not bring any information as to the identity of their husband's clan.

[150] Alternatively, this may be another evidence for a two-pronged introduction of manioc into northern Gabon, as suggested by the **afouba**/**akwama** linguistic dichotomy. In Mbong-Ete, farmers have two words to designate sweet manioc, **afouba** and **akwama**. While the former evokes a connection with the **afobo** of the Yasa [A.33a] from south-western Cameroon (see Dounias 1993), the latter suggests a faraway relation to the **dikwãmba**[*] of the Duala [A.24] (see Rossel 1987), suggesting manioc may have been introduced into northern Gabon at least two times, independently. The two clones, G5 and G14, may be each associated with different diffusion routes.

[*] **Ikwãmba** is also the generic name in Galwa [B.11b] for sweet manioc (see Chapter III).

In fact, the low number of distinct landraces in Mbong-Ete was not strictly matched by low genetic diversity. Although allelic diversity in Mbong-Ete was significantly lower than that found in the other villages studied, none of the three landraces was completely monoclonal, and I found overall higher levels of genotypic diversity than I expected given the low number of named landraces.

There are at least two hypotheses that could be proffered to explain this mismatch between the expected and the observed levels of genetic diversity: 1) Ntumu folk taxonomy is loose, and farmers underestimate the actual diversity in their farms; or 2) volunteer seedlings are regularly incorporated into the stock of cuttings. A loose definition of landraces is however not consistent with the high agreement and high consistency levels I found in Mbong-Ete.

Conversely, the highest manioc seedling densities ever reported[151] were observed in Mbong-Ete, where volunteer densities reached up to 9 seedlings $\times m^{-2}$. Ntumu farmers systematically pull out manioc volunteers because they hinder the development of peanuts, which precede manioc in the crop sequence. However, the exceptionally high densities of volunteers in their farms increase the probability that seedlings are accidentally incorporated to the stock of cuttings. No matter how careful farmers are in weeding their farms, accidental incorporation of seedlings thus seems the principal mechanism through which genetic diversity can be maintained in Mbong-Ete.

### 4.4.1. Seedlings and allelic diversity

Formerly, Fang villages were itinerant and changed location as soon as all land around had been cultivated (Carrière 1999). The construction of permanent structures such as schools and dispensaries along roads in the 20th century aimed at breaking with this mobility and at fixing communities (Carrière 1999, Knight 2003), but perturbed the traditional equilibrium between villages and their environment (Mbot 1997), forcing farmers to introduce a rotation of land occupation[152]. Now, every five years or so, farmers have to return to their old parcels. Manioc seeds from these repeated cycles of cultivation accumulate in the soil, constituting, with time, important seed banks.

[151] In Africa and Amazonia alike. See in particular Elias and McKey (2000), McKey *et al.* (2001) and Pujol *et al.* (2005a). Such data for Africa are scarce, but the values found in Mbong-Ete are still extremely high.

[152] The technique of the fallow (**ekoro**) has long been practiced in the region (Dounias 1993, Mbot 1997, Carrière 1999). However, the limited availability of new lands around the village implies that farmers must return more often to the same plots.

When farmers clear a parcel, the removal of vegetation stimulates the germination of manioc seeds (Elias & McKey 2000, Pujol *et al.* 2002, Pujol & McKey 2006). Volunteers could be observed in large numbers in every field. Most seedlings emerge within two weeks after burning (Elias & McKey 2000, Pujol *et al.* 2002), but germination can be spread over several months (Raffaillac & Second 2001). Even after they had patiently weeded their farms, farmers still found some volunteers while sowing peanuts, so that when it was time to plant manioc cuttings, the Ntumu had to weed their farms again. Once peanuts had been harvested, though, fields were not weeded anymore.

A manioc farm can be harvested over two or three years, depending on its size, until all roots have been harvested or until weeds have completely invaded the parcel. Seedlings may emerge even while the farm is still producing, and indeed volunteers were frequently observed in older farms[153]. It is then not excluded that seedlings may accidentally end up being incorporated into the stock of cuttings when farmers harvest stakes in preparation for planting the next set of farms. How often seedlings are incorporated is difficult to evaluate, but considering the huge number of manioc volunteers in Ntumu farms[154], the frequency of casual inclusion of volunteers in the stock of cuttings is certainly not negligible. It seems likely that the regular re-injection of new genotypes through the accidental incorporation of seedlings contributed to balance the loss of genotypic diversity through the sieve of selection of stem cuttings, although this was not enough to prevent some alleles being lost.

### 4.4.2. Contribution of landraces to sexual reproduction

Allelic composition of seedlings collected in $K_2$ showed limited allelic diversity. Data also suggested that '*Adzoro*' contributes more than the other two landraces to sexual reproduction. Parent-offspring analyses rejected '*Esobo-Nku*' and '*Akwama-Mbõng*' as the potential mothers of most of the seedlings collected in $K_2$, and identified G5, in particular, as the most likely mother of the majority of the volunteers.

[153] They usually grow straight and stand out from the landraces, which, in contrast, are highly branched. However, in old farms where farmers harvest stems to prepare cuttings, manioc plants are tall (three to four metres) with low leaf cover density, and it may be difficult to differentiate volunteers (see Sambatti *et al.* 2001). In Amazonia, farmers identify older volunteers by their short basal internodes and single taproot (Pujol *et al*. 2005a). In Mbong-Ete, farmers only noticed that volunteers grew alone, while cuttings produce several stems.

[154] The average density I found would correspond to about 30,000 seedlings per hectare, that is, three times more than there are actually cuttings planted in a farm!

Farmer NOL, from whose farms seedlings were collected, did not grow the genotype G14, which explains why most seedlings could be offspring of G5, but not of G14. This fact probably also explains the overall limited allelic diversity within the cohort of seedlings. Volunteers were collected in $K_2$ shortly after the plot was burned, so that farmers had not started yet to weed the farm. The sample was therefore expected to represent the genetic structure of the cohort prior to any selection. I found no significant deficit of heterozygotes within the cohort of seedlings. Selfing accounted for approximately 20% ($s = 0.199$), which may simply reflect the dominance of '*Adzoro*' in the production of seedlings.

The relatively small sample size ($N = 31$) may partly explain the dominance of '*Adzoro*' as the potential progenitor of most volunteers collected in $K_2$. Testing for any difference in fecundity between Ntumu landraces would have required sampling more seedlings from over a larger number of plantations[155]. However, planting patterns were very homogeneous in the village, and '*Esobo-Nku*' dominated in all farms (about two cuttings of '*Esobo-Nku*' for one cutting of '*Adzoro*'), and sweet manioc represented only about one sixth of the total area planted with manioc. Thus, the higher probability that seedlings are offspring of the landrace '*Adzoro*' could not be explained by a difference in planting densities. Besides, the proportion of atypical genotypes was much higher in '*Adzoro*' than in any other landrace. More than 20% of plants of '*Adzoro*' showed unique genotypes (while it was only 7% for '*Esobo-Nku*' and 10% for '*Akwama-Mbõng*'), suggesting frequent and repeated incorporation of plants issued from seeds.

The analysis of the structure of genetic diversity within the cohort of seedlings hence supports the hypothesis that '*Adzoro*' contributes more to sexual reproduction, either by (1) higher fecundity (higher production of fruits and seeds), (2) higher germination rate of seeds produced by '*Adzoro*', or (3) better survival abilities of seedlings[156].

[155] Sampling of volunteers was however strongly constrained by the timing of fieldwork. Surveys started in September, while most fields had been cleared the month before, and farmers were already planting peanuts. Most farms had already been weeded at least once.

[156] An analysis of the allelic composition of seeds randomly collected on the ground and an estimation of the proportion of seeds produced by '*Adzoro*' in comparison to the proportion of seeds produced by the two other landraces would allow the potential difference in fecundity between the three Ntumu landraces to be evaluated. If the difference is not in the number of seeds produced by each landrace, but in their ability to germinate or their rates of survival, then germination experiments in controlled environment would be necessary.

### 4.4.3. The particular case of '*Adzoro*'

All Ntumu landraces were branched and bore large numbers of fruits. In *M. esculenta*, branching is induced by flowering[157]. The fecundity of a landrace, in other words its propensity to produce fruits and seeds, is thus related to its degree of ramification (Jennings 1995, Elias 2000, Elias *et al.* 2007).

Unlike the other two landraces which branch tardily, '*Adzoro*' formed small and dense shrubs, which contrasted with the tall and straight stems of '*Esobo-Nku*' and '*Akwama-Mbõng*'. '*Adzoro*' had a higher level of branching and an overall shorter primary stem, suggesting that it branches—and thus flowers—earlier but also more often than '*Esobo-Nku*' and '*Akwama-Mbõng*'. Early and higher flowering gives '*Adzoro*' an advantage over the two other landraces in terms of contribution to sexual reproduction. In the same period of time[158], '*Adzoro*' will flower more often and thus produce a larger number of seeds. However, early branching also gives '*Adzoro*' an indirect 'advantage' over the two other landraces in terms of clonal propagation.

Because '*Adzoro*' is generally smaller than the other two landraces, farmers need to harvest a higher proportion of plants in order to obtain the same number of cuttings. Where from an average stem of '*Esobo-Nku*' farmers would make three or four cuttings[159], only one or two cuttings can be made out of a stem of '*Adzoro*'. Farmers adjust for this loss of exploitable material by harvesting more plants. The corollary is that more genotypes of '*Adzoro*' are propagated, while for the two other landraces, many are lost. This 'size-effect' (see Elias *et al.* 2007) contributes to reduce the bottle-neck effect associated with the selection of planting material, and probably results in a larger number of genotypes being maintained through clonal generations.

Comparison of the genotypic structure of landraces indeed showed for most landraces a large dominance of a single clone, the few others being represented by only a couple of plants. For '*Adzoro*', two major genotypes coexisted[160], along with a large number of individuals showing unique genotypes (singletons). The monolithic genotypic structure of

[157] See Chapter I.

[158] That is, while the field is producing, so over a period of two or three years.

[159] Setting 50 cm as the average length of cuttings, and taking into account the reduction of the diameter of the stem subsequent to branching (Hallé *et al.* 1978). The length of usable primary stem is thus considerably reduced in the case of '*Adzoro*'.

[160] The bimodal genotypic structure of '*Adzoro*' is however unlikely to be the consequence of a reduced bottleneck, owing to the pattern of distribution of genotypic diversity between farmers.

'*Esobo-Nku*' suggests in contrast a stronger bottleneck effect, which partly explains the lower genotypic diversity and the lower allelic diversity I found for this landrace. The fixation or near-fixation of several alleles in '*Esobo-Nku*', and the very low frequencies of several other alleles commonly found in the two other landraces, are all indicative of a phenomenon of genetic erosion which affects the landrace '*Esobo-Nku*'. In the case of *Akwama-Mbõng*, the coexistence of genetically differentiated morphotypes ('*Matati* a', b, c and d) contributes to enrich its genetic pool, even if this contribution is rather limited.

Two opposite dynamics, one strengthening the bottleneck effect, the other one preserving genetic diversity, act simultaneously in Mbong-Ete. On one hand, the system preserves, although to a limited extent, a rather high level of allelic and genetic diversity despite a limited array of landraces. On the other hand, it also constrains genetic diversity within the boundaries of the village, by proscribing exogenous imports of planting material, and rebuffing any new landrace coming from outside the village.

## 4.5. The diktat of yield

Risk aversion is a significant driving force in traditional farming systems, and dictates significantly farmers' behaviour and decisions (Peroni & Hanazaki 2002). Most of the manioc produced in Mbong-Ete is destined to be sold in the form of *bâtons* on the market in Bitam. In a system so dependent on manioc marketability and putting so much emphasis on yield, it is essential for farmers to preserve the integrity of their landraces, in particular those of higher economic value ('*Esobo-Nku*').

Exerting strong ideotypic selection on planting material and systematically pulling out manioc volunteers are two strategies commonly used by manioc farmers to maintain their landraces "true-to-type" (see Manu-Aduening *et al.* 2005). In Mbong-Ete however, weeding manioc volunteers is mainly dictated by agronomic considerations.

Because they may have a detrimental effect on the growth of peanuts, especially in the first few weeks of the plantation, manioc volunteers represent a threat to peanuts. They do not, however, imperil manioc itself. This important difference with, for instance, Teke [B.71] farmers in south-eastern Gabon who reject seedlings because they do not look like a landrace they know[161], or with Tsogho [B.31] farmers who discard volunteers because

[161] Teke farmers exert a selection based on perceptual indistinctiveness. They favour volunteers with recognizable morphological characters, and discard, in contrast, those with variant morphotypes (Delêtre & McKey submitted).

they represent a risk of poisoning[162], may relax weeding pressures on volunteers in Ntumu farms when no peanuts are grown, and increase the odds that seedlings will be accidentally incorporated into the stock of cuttings.

A third strategy to preserve the genotypic integrity of a landrace is to favour the continuation of landraces strictly within the family nucleus, through a codified system of transmission of cuttings down the successive generations of farmers. In a patrilinear and virilocal system, affinal transmission is the sole system which ensures the preservation of the landraces' gene pools. However, by disconnecting villages from regional exchange webs, the Ntumu kinship system also cancelled the "buffer effect" (Peroni & Hanazaki 2002) of dynamic exchanges of planting material, maintaining genotypic diversity at the village scale at a risk of genetic erosion. Alleles, alongside genotypes, are lost every time farmers select plants for the next farming season. Genetic diversity is only partly salvaged by the ecological opportunities created by the farming system for the accidental incorporation of manioc volunteer seedlings, but does not suffice to compensate for the slow erosion of allelic diversity[163].

**Synthesis**

Manioc varietal diversity in northern Gabon is exceptionally low, and has long remained so. The very limited range of manioc varieties found in Ntumu farms is the result of an initially limited availability of varietal diversity, constrained by the interventionism of colonial authorities. The late start of manioc cultivation in the region from an initial low number of landraces suggests that today's picture of manioc diversity in northern Gabon has changed little over the last century. Diversity remained at a standstill, helped in this respect by the social organisation and material culture of the Ntumu.



[162] See Chapter IV.

[163] Allelic diversity was probably also initially low. The overall lower allelic diversity I found in northern Gabon (see Appendix C4) suggests that despite the probable multiple introductions of manioc from Cameroon, as suggested by the variety of names found for sweet manioc in Mbong-Ete, the landraces introduced from the West Indies into Cameroon in the 1890-1910s (Mouton 1949) represented only a limited allelic diversity.





**Plate V**

Twice a year, Ntumu farmers clear large forest plots (a), where they generally grow peanuts which they intercrop with manioc. Because peanuts require a perfectly clean soil, farmers spend a long time after burning to weed their fields and remove any roots or branches left after clearing (b).


**Plate V** (continued)

Ntumu farmers always plant peanuts first (c). Two weeks later, peanuts are intercrop with manioc (d). Single stem cuttings are planted diagonally, about one meter apart. Farms are weeded twice, before peanuts are planted and when planting manioc. Manioc volunteer seedlings are treated as weeds, and systematically discarded. Volunteers can be recognized by their short basal internodes (e) and single taproot (f), but generally farmers only notice volunteers because they grow alone, while cuttings produce several stems.

# Chapter VI

## *Beyond the names:*
## *From the concept of landrace to its implementation in the field*

# 1. The multiple facets of manioc 'cultural domestication'

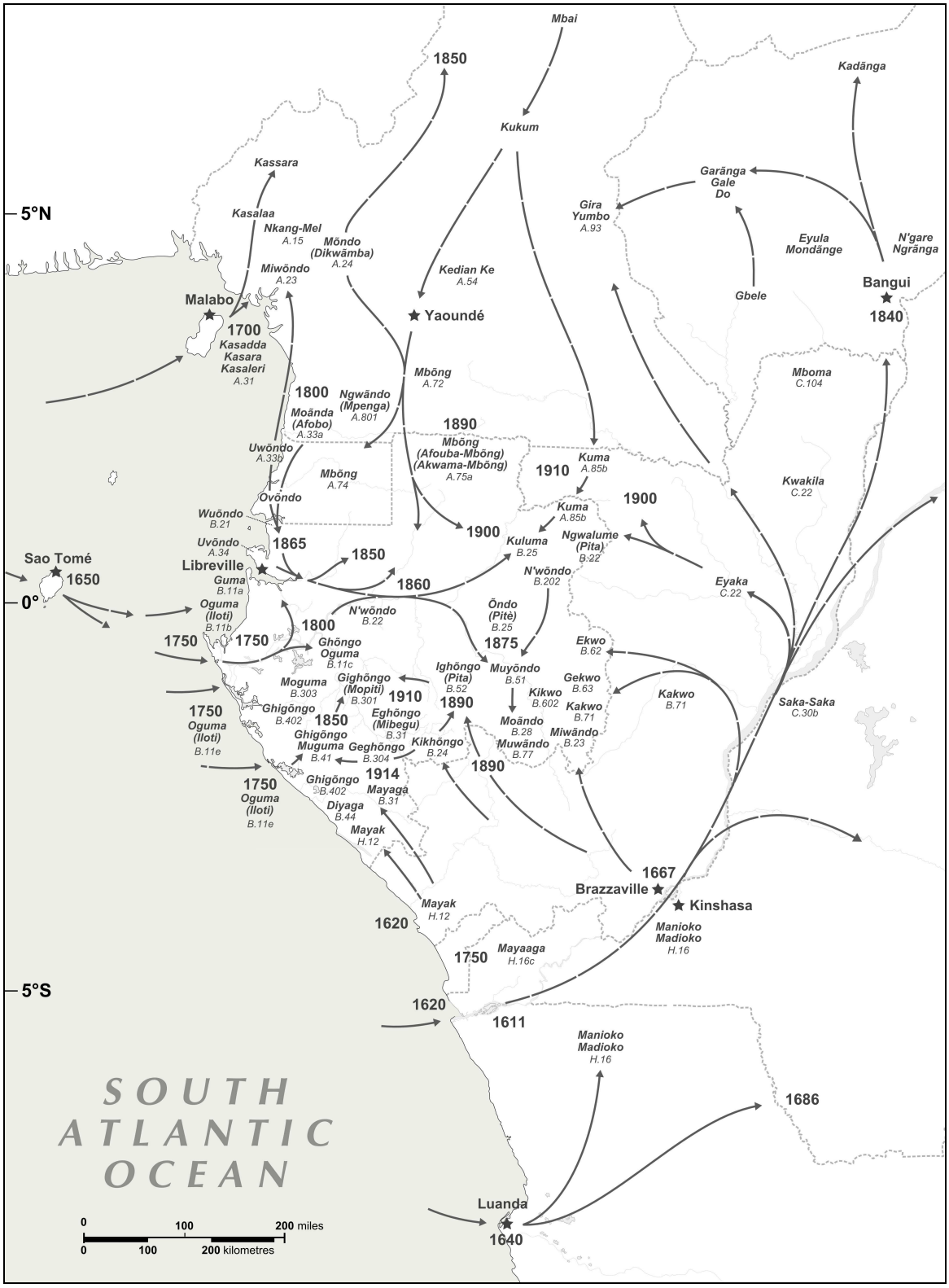
The diversity of manioc farming systems I have documented in the previous chapters shows that there isn't just one history of manioc in Gabon. There are, in fact, as many different histories as there are names for the crop. Each is the local expression of a single underlying process of cultural domestication, which depended greatly on the context of adoption of the crop, and contributed, to various extents and in different ways, to building the soaring diversity of manioc in Gabon.

I have shown that manioc probably followed several different routes in spreading into Gabon (Map 6.1). Each of these multiple introductions participated jointly with the cultural processes of 'domestication' that accompanied the adoption of manioc by the populations in shaping the patterns of manioc diversity in Gabon.

On the coast, multiple and repeated introductions most likely occurred throughout the one hundred years of intensive commercial exchanges between the Myènè [B.11] and São Tomé. This would have favoured the accumulation of diversity along the coast, magnified by the particularly positive attitude of Myènè farmers towards novel forms that appear in their farms (see Chapter III). In Odimba, unfortunately, such diversity had been recently superseded by a monotonous array of monoclonal varieties. I believe, however, that deepening the investigation of manioc in this region of particular importance in the history of its spread would yield more data supporting the existence of a particularly rich and active 'hotspot' of diversity in the delta of the Ogooué and the region of the lakes.

In northern Gabon, the particular social organisation of the Ntumu [A.75a] society, combined with an initially low availability of useful genetic diversity, maintained low varietal and low allelic diversity, and the trace of the founder effects associated with the probable re-introduction of manioc in Gabon from Cameroon in the second half of the 19$^{th}$ century (see Chapter V).

In this chapter, I followed two lines of discussion, which represent the two dimensions of the reciprocal interaction of the plant and farmers. Drawing from my conclusions from the three case studies I analyzed firstly how "people affect plants" (Salick 1995). Secondly, I generalized my conclusions to the enlarged study of plant-people interactions, showing that much can be learned in the areas of crop introductions from studying crop diversity while keeping in mind that plants, also, can affect people.




**Map 6.1. Reconstruction of the historical pathways of manioc diffusion into Gabon**, with a proposed timeline for the onset of manioc farming in the different regions of Gabon. Adapted from Rossel's (1987) analysis of manioc vernacular names in Central Africa. Both terms for bitter and sweet manioc are given (sweet manioc is indicated between brackets). Bantu languages are denoted following Maho's (2003) proposed revision of Guthrie's classification of Bantu languages (Guthrie 1948).

## 2. People affect plants

Models of the evolutionary dynamics of clonally propagated crops have underlined the role of the incorporation, conscious or unconscious, of recombinant plants from sexually produced seeds for the maintenance of high levels of genetic diversity (Brush *et al.* 1981, Johns & Keen 1986, Cury 1993, Sambatti *et al.* 2001). However, no study to date had examined in detail how folk ecology interacts with historical, socio-economic and environmental factors to influence the perception of manioc volunteer seedlings as a source of diversity.

The diversity of farmers' behaviours towards manioc volunteers that I have documented in Gabon illustrates the complexity that may be found in comparative studies of the role of volunteer seedlings in the evolutionary dynamics of clonally propagated crops. It also shows that the constitution and renewal of stocks of germplasm are channelled by knowledge and beliefs, and by social or cultural representations and valuations of diversity which are specific to each community. Pinton (2003) summarized in two categories farmers' perception and use of diversity:

1. The experimental approach, which is the one practiced by the Amerindians (see Boster 1984a, 1984b, Salick *et al.* 1997, Elias *et al.* 2000a), where diversity is dynamic and culturally highly valued;
2. The selective approach, which, in contrast, focuses on a restricted set of landraces, chosen for their performances. Here also, diversity can be dynamic, in the sense that landraces can be interchanged, with some being replaced by others as farmers' needs and wants evolve.

Behaviours intermediate between these two extremes also exist, but the choice for a society to evolve towards the experimental or the selective approach depends, as I have shown, as much on internal pressures (social or cultural valuation of diversity) as on external pressures, including ecological, social, economic, and historical factors.

I have so far explained how farmers in Gabon perceive manioc diversity, and how they used named landraces as the basic units of management of diversity in their farms. Using the formalistic approach proposed by Cleveland *et al.* (2000), I will re-introduce the concept of landrace into the evolutionary model of the dynamics of manioc genetic diversity, in order to comprehend the role of farmers-plant interactions in the dynamics of manioc genetic diversity.

## 2.1. A dynamic construal of the concept of landrace

Cleveland *et al.* (2000) have proposed a formalistic definition of the landrace, which can be defined as an equation:

$$V_P = V_G + V_E + V_{G\times E}$$

where $V_P$ is the phenotypic variation, $V_G$ the genetic component of variation, and $V_E$ the variation linked to the environment, and the component $V_{GxE}$ represents the interaction between genetic variation and environmental variation. Farmers do not perceive genetic variation ($V_G$) but act on it through the way they manage phenotypic diversity ($V_P$) with regard to the environment ($V_E$), and learn from continuous observation the norm of reaction of each of their landraces, that is, $V_{GxE}$. This learning process is dependent on farmers' perception of diversity, that is, the rules they apply to 'discretise' diversity into phenotypically distinct units and into culturally defined entities (see Friedberg 1973).

The criteria used by farmers for classifying individual plants into distinct landraces cannot be formally described, as the process of recognition of a landrace is based not on the identification of a discrete list of properties, but rather is generally based on the immediate and comprehensive perception of a set of morphological characteristics, which together form the "Gestalt" of the landrace (d'Andrade 1995). This process was compared by Shigeta (1996) to "face-to-face recognition".

Maintaining the adaptability of farming systems to $V_E$ is key to preserving their resilience. While encouraging diversity in their manioc farms, farmers accumulate a stock of landraces widely diversified in their agroecological requirements, which confers to the system its flexibility and dynamicity (Altieri 1999, Peroni & Hanazaki 2002, Di Falco & Perrings 2003), and which can be repeatedly evaluated through trials and selected upon.

In Gabon, farmers continually seek new manioc landraces to try, leading to an accumulation of landraces over time. The diachronic comparison of the levels of diversity found in the manioc farms of the Myènè Galwa [B.11c] in Nombedouma (Chapter III) and the Tsogho [B.31] in Douani (Chapter IV) has shown that farmers accumulate landraces over time, rather than replace them, and some landraces grown in the 1960s are still grown today (*e.g.*, '*Putu*', '*Matadi*', '*Pauline*', '*Oyogho*', '*Regholoto*', '*Evizovizo*', '*Ayumbo*', '*Ikwãmba*', '*Ngwesuku*'; see Chapter III).

In a previous study among the Teke [B.71] farmers in south-eastern Gabon (Delêtre 2004, Delêtre & McKey submitted), I have shown that the dynamics of diversity in manioc farms reflect the continuous selection by farmers of the most appropriate sets of landraces, to cover the range of ecophysiological heterogeneities that may be found in their farms (variations in the composition of the soil, in water availability or in herbivore pressures). The choices made by farmers to maintain high levels of diversity are therefore partly 'tuned' to the local agroecological and/or socioeconomic environment. I showed however that such an experimental approach feeds on diversity, and that farmers continuously seek new varieties to try.

The Teke are no exception in Gabon. While constantly experimenting, trying new varieties and modifying the varietal composition of their farms, farmers in Gabon accumulate landraces, explaining why I found exceptional levels of diversity in most of the villages I surveyed. The case of the Tsogho [B.31], who accumulated over the years a large collection of varieties of sweet manioc, shows clearly that the "push to collect" (Heckler & Zent 2008) that characterizes Amerindian farmers (Emperaire *et al.* 1998, Elias *et al.* 2000a, Rival 2001) is also widespread in Gabon. Such active compilation of landraces resulted in local concentrations of diversity, which I termed "passive hotspots" of diversity[164]. Beyond this experimental approach, diversity was also favoured *per se*, without any preconception about its potential usefulness. Landraces have a strong social and patrimonial value (Shigeta 1996, Elias *et al.* 2000b, Heckler & Zent 2008), and farmers in Gabon also maintained 'heirloom' landraces by attachment to their older varieties, even though they considered them as obsolete. Examples include '*Putu*' in Odimba (Chapter III) and '*Õndzalapaki*' in Odjouma (Delêtre 2004).

[164] See definition in Chapter I.

It is however essential for farmers to remain able to discriminate between this large diversity of types, in order to learn about their different varieties and select the landraces—or combinations of landraces—most appropriate for a given environment.

When I assessed the biological dimension of folk taxonomies, I found that names of landraces rarely reflected a discrete genetic identity (with the particular exception of the Myènè in Odimba), and that most landraces encompassed, instead, a large group of genotypes. Surprisingly, I found little to no overlap between named categories, suggesting a remarkable degree of consistency between farmers' naming of landraces at the community level. Farmers rarely disagreed on a name[165], and while allowing for occasional mistakes when identifying landraces in their farms[166], their folk nomenclature systems appeared coherent, suggesting that despite mechanisms that contribute to increase genetic diversity locally, other mechanisms permit preservation of the 'integrity' of a landrace, and the maintenance of high levels of genetic differentiation between landraces.

## 2.2. Landraces as a perceptual 'tool'

Maintaining large numbers of landraces implies that farmers must remain able to discriminate between their landraces, hence that the Gestalt of each landrace is preserved. Maintenance breeding (Zeven 2002) entails a particular type of selection, termed ideotypic selection, that aims at controlling $V_P$ as a tool to learn about landraces and their reaction to $V_E$ (that is, $V_{GxE}$). In Gabon, ideotypic selection governed to a large extent farmers' behaviours towards manioc volunteers, and depended, in turn, on farmers' intimate knowledge about manioc volunteers.

### 2.2.1. Watching and learning

Folk knowledge is constrained by farmers' opportunity to observe, and thereby to learn about manioc reproductive biology. Agroecological factors are, in part, responsible for the variation among farmers in their knowledge about manioc volunteers. Among Teke [B.71] farmers, in south-eastern Gabon, I showed that the ecological opportunities created by the farming system itself can constrain farmers' opportunity to observe manioc volunteers, and thereby their knowledge about manioc's ability to reproduce sexually (Delêtre 2004, Delêtre & McKey submitted).

[165] See however an exception in Chapter IV.

[166] Genuine mistakes usually represented less than 5% of the samples I collected in each village.

### *The Teke dual farming system*

The Bateke plateaux, a territory mostly covered by low shrubby savannah with scattered fragments of forest, extend over 500 km from north to south and 250 km from east to west, across Gabon, the Congo Republic, and Congo Democratic Republic. Responding to the ecological constraints imposed by their forest/savannah ecotone habitat, the Teke [B.71] have created a unique farming system based upon agroecological duality, where manioc is cultivated in two spatially and ecologically distinct systems, the savannah system, **ntsege**, and the forest system, **ngunu**.

Every year farmers open new fields both in savannah and forest. In savannah, as land is abundant and demographic pressures are low, farmers avoid old fallows and favour instead 'pristine' land to open new farms. Lower intensity of land use results in lower density of soil seed banks in savannah. In contrast, shortage of land in forest compels farmers to return regularly to old fallows. Field preparation, including burning, favours the germination of seeds produced during the previous cultivation cycles in forest. Seedlings were significantly more frequent in Teke forest farms. Consistent with this observation, while 43% of the farmers I interviewed in Odjouma reported that they had never found volunteers in their farms[167], the other 57% reported that they had observed volunteers, but only in their forest farms (Delêtre 2004, Delêtre & McKey submitted).

Hence, the cleavage into two separate farming systems seems to have constrained Teke folk knowledge about manioc ecology. In Ghana, Manu-Aduening *et al.* (2005) similarly observed great variation among Ghanaian farmers in their knowledge about manioc volunteers, and found a significantly higher proportion of farmers that had never observed volunteer seedlings in farming systems where soil was mechanically ploughed, than in those were the soil was simply hoed. Thus, the organisation of the farming system (land management and fallow systems) and the farming practices, such as burning the farms or the techniques of preparation of the soil prior to planting (ridging, hoeing or ploughing) can have a direct impact on farmers' *experience* of manioc volunteers, and constrain their folk knowledge about manioc ecology.

[167] See Figure 2.5 h in Chapter II.

### 2.2.2. Doing

Folk knowledge determines, in turn, farmers' appreciation of the positive or negative value of manioc volunteers, and influences the strength and direction of the selection they apply on manioc volunteers. The perception of manioc volunteers by Gabonese farmers could be broadly summarized into four categories: 1) "safe", 2) "worthless", 3) "deceitful", and 4) "harmful"[168]. The categorization by farmers of manioc volunteers into these four different classes reflects, as I have shown in the three case studies, culture-dependent differences in valuation of diversity, driven in some instances by historical constraints on the diffusion of the technologies associated with manioc farming, in particular the adoption, or not, of techniques to detoxify manioc roots.

Volunteers were often deemed "worthless" because farmers noticed they only produced a taproot instead of the the adventitious roots which usually develop from cuttings, and in some cases "harmful" because they grew to the detriment of other crops, as in the case of the Ntumu [A.75a] in Mbong-Ete who discarded volunteers because they compete with peanuts[169] (Chapter V). In Douani, the Tsogho qualified volunteers as 'deceitful'[170], and systematically discarded them, because they could not rely on them to have stable agronomic and/or organoleptic properties, in particular relating to bitterness (Chapter IV). These various rationales governed farmers' choice to foster or discard volunteers in their farms, and led to a variety of forms of selection that impinged on the dynamics of manioc diversity. Basing my discussion on an evolutionary model of manioc genetic diversity presented in Figure 6.1, I will analyze below how farmers interact, directly or indirectly, with the plant's biological and ecological traits.

[168] See Figure 2.6 in Chapter II.

[169] Alternatively, the limited array of genotypes in Ntumu farms implies that geitonogamy is also more frequent, as the analysis of the genetic diversity of seedlings collected in $K_2$ suggests. Because manioc suffers from strong inbreeding depression (Pujol & McKey 2006), wherever varietal diversity is low inbred volunteers may be more frequent. This may alter farmers' perception of manioc volunteers and modify their behaviour. If volunteers look stunted, farmers will be more inclined to discard them.

[170] And potentially harmful, because unfit for consumption.

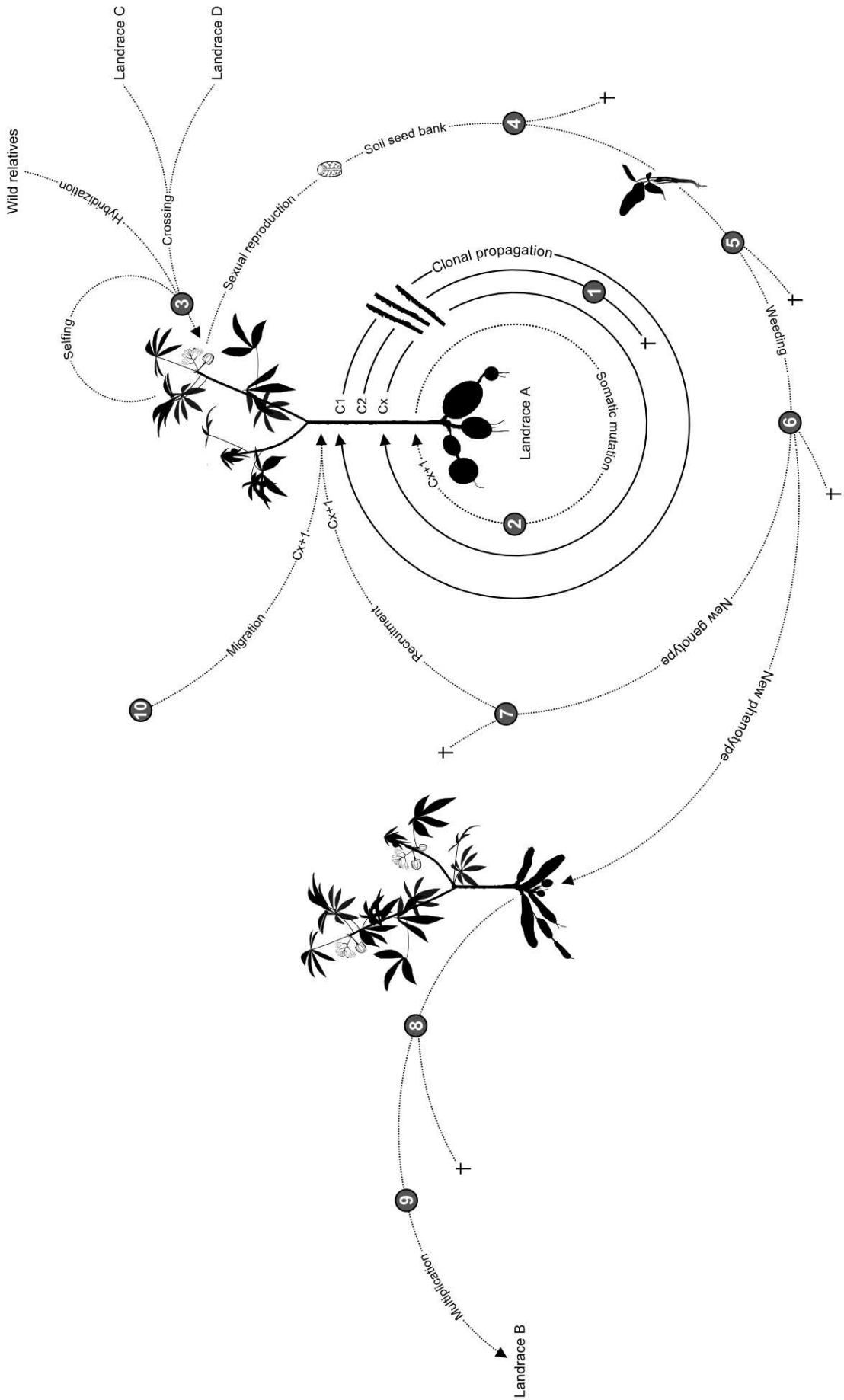



**Figure 6.1. An evolutionary model of manioc genetic diversity**. Farmers interact with the plant's biological traits on ten particular points (see discussion).

# 3. The dynamics of manioc genetic diversity

The first model of the evolutionary dynamics of manioc diversity was proposed by Cury (1993). While the model has since been modified and enlarged (Sambatti *et al.* 2001, da Silva *et al.* 2003, Rival & McKey 2008), it has been little tested in the field, more so in the African context. The large comparative survey I undertook in Gabon provides a large array of contrasted situations that can be used as practical examples to discuss the interactions of farming practices with manioc biological traits.

## 3.1. Selection of planting material and genetic bottle-neck

The dynamics of manioc genetic diversity can be thought as a mixture of processes that decrease genetic diversity, such as the bottle-necks associated with clonal propagation (Balloux *et al.* 2003) and the natural loss of allelic diversity due to genetic drift, and processes that increase genetic diversity, through the fixation of somatic mutation or the migration of germplasm through the exchange of cuttings, or through the recruitment of self-sown volunteer seedlings.

The first phase of the model is the preparation of the propagules ❶, that is, the selection by farmers of the stakes that will be used to prepare stem cuttings for the next farming season. Because of their need to minimize $V_P$ within landraces, farmers tend to duplicate only the plants with the most 'typical' characteristics of a given landrace (Elias *et al.* 2001a, Sambatti *et al.* 2001, Mkumbira *et al.* 2003, Kizito *et al.* 2007), choosing stems on the basis of a set of criteria that includes conformity to farmers' ideal phenotypic representation of the landrace (*i.e.*, ideotype, *sensu* Duputié *et al.* 2009) and absence of any obvious signs of infection. Because several cuttings can be made of a single individual, only a sub-sample of the plants is necessary to renew the stock of propagules. Elias *et al.* (2000b) estimated that only about 10 to 15% of plants in a farm are recruited each year to renew the stock of germplasm, meaning that between two successive farming cycles, more than 80% of plants are not propagated.

### 3.1.1. "Size does matter"

As I illustrated in Mbong-Ete (Chapter V) with the particular antagonism between the landraces '*Adzoro*' (small, highly branched) and '*Esobo-Nku*' (tall, straight), the architectural parameters of manioc landraces can contribute to moderate, or to accentuate, the effect of this genetic bottle-neck.

Selection of planting material is based on subjective criteria regarding the quality of the stem, including physical characteristics such as the diameter of the stem. In manioc, propagule quality is dependent on the starchy reserves that can be mobilized by the plant to develop new roots and new shoots from the cutting. The critical parameter, therefore, lies in the mass, which farmers adjust by chopping longer or smaller pieces of stem, depending on the diameter of the stem (Elias *et al.* 2007).

In manioc, there is a strong relationship between the degree of ramification of a landrace and the multiplication factor, that is, the clonal fecundity of the landrace (Elias *et al.* 2007; see Chapter I). Because the primary diameter of the stem decreases each time the plant branches, the higher the degree of ramification, the longer a stem cutting must be to have enough reserves to survive and grow[171]. As in the case of '*Adzoro*', farmers can adjust for this loss of exploitable material by harvesting more plants, thereby propagating more individuals. Landraces are therefore unequal in terms of "clonal fecundity", and the taller plants are more prone to suffer from a stronger bottle-neck than landraces that stay small or branch often.

### 3.1.2. "Tell me how you plant, I'll tell you who you are"

In Gabon, planting techniques—*i.e.*, the number as well as the disposition and orientation of manioc cuttings—varied greatly between communities, and was a very distinctive trait of manioc farming among a particular ethnic group (*e.g.*, the Ntumu [A.75a] used only one cutting, while the Tsogho [B.31] used three cuttings and the Myènè [B.11] used generally four cuttings).

Beyond the evident expression of the diversity of forms cultural domestication can take, variation in the number and characteristics of cuttings has a direct incidence on the number of cuttings that will be required to plant a new farm, hence on the number of plants that will be recruited for the next clonal generation.

In theory, the strength of bottleneck effects should decrease as the length of cuttings increases, since the longer the cutting, the smaller the number of cuttings that can be made from a single stem. However, genetic diversity will increase if the number of cuttings augments. Although I have not specifically studied the impact of planting techniques on genetic diversity, my data seem congruent with a moderator effect of planting techniques on the strength of the bottle-neck.

[171] Elias (2000) found that below 1 cm of diameter, cuttings wither and die.

## 3.2. Somatic mutations

While some genotypes are lost, some natural autochthogenous forms of diversity may appear through new mutations ❷. Fixation of somatic mutations is however a very slow process. While it apparently played a significant role in the diversification of the taro (*Colocasia esculenta*) in Vanuatu (Caillon *et al.* 2006) and of bananas in East Africa (Pickersgill 1998), the fixation of somatic mutations is limited, in the case of manioc, by the strong genetic bottle-neck associated with clonal propagation, and cannot alone explain the amount of genetic diversity encountered in African manioc populations.

## 3.3. Sexual reproduction and hybridization

Sexual reproduction ❸ has played a major role in amplifying diversity in manioc populations managed by Amerindians (Sambatti *et al.* 2001, Salick *et al.*, 1997, Emperaire *et al.* 1998, Elias *et al.* 2000a, McKey *et al.* 2001, Pujol *et al.* 2005b) but also in other areas where manioc was introduced, *e.g.*, in Vanuatu in the south-western Pacific (Sardos *et al.* 2008).

Despite the importance of the crop for Africa, and, in turn, the importance of Africa for the crop[172], few data are available on the contribution of the sexual component of manioc reproductive biology to the demography of manioc in Africa. No authors have attempted—beyond speculating on the possible role of the incorporation of manioc volunteers (Fregene *et al.* 2000, 2003, Kizito *et al.* 2005, 2007)—to document the behaviours of African farmers towards manioc self-sown seedlings (but see Manu-Aduening *et al.* 2005). Moreover, no previous study explored this question by combining an ethnobotanical and a genetic approach. One of the aims of this thesis was to contribute to fill this gap.

### 3.3.1. Gene flows between landraces

Populations of manioc are usually highly heterozygous (Kawano *et al.* 1978). The plant is monoecious, but has a reproductive system predominantly allogamous (Raffaillac & Second 2001). Female flowers open five to eight days before male flowers. Protogyny favours outcrossing, and experimental crosses in a garden composed of different landraces have shown that the multilocus outcrossing rate averages 90% (da Silva *et al.* 2003).

[172] Africa is now the first ranking manioc producer in the world (FAO 2009).

Each manioc plant can produce between one and six fruits per inflorescence, but the number of inflorescences itself is governed by several factors, including environmental factors. Rich soils can inhibit flowering, while poor soils can promote flowering (Raffaillac & Second 2001). There is also high variation between manioc landraces in their ability to produce functional flowers. Some landraces may flower up to ten times over a single year, while some others will not flower at all.

In Chapter V, I suggested that such intervarietal variability in sexual fecundity was the most likely explanation of the dominance of one landrace, '*Adzoro*', as the potential progenitor of most volunteer seedlings collected in one Ntumu farm. Analyses of the genotypic diversity in Ntumu manioc landraces similarly showed a higher number of atypical genotypes in '*Adzoro*', suggesting that sexual reproduction plays an important role in the ecology of this particular landrace.

### 3.3.2. Selfing

Manioc is also capable of autogamy (Kawano *et al.* 1978), and self-pollination also occurs in farms (geitonogamy[173] was estimated to be about 20% in the population of volunteers sampled in Mbong-Ete, and similar values were obtained by David *et al.* 2007 and Duputié *et al.* 2009b in Palikur and Wayãpi manioc farms, respectively).

The composition of the farm (number of landraces and relative area planted with each landrace in the farm) and the spatial configuration of varietal plots in the farms (planting pattern) are two factors that can either favour outcrossing or favour selfing (Pujol *et al.* 2005b). In monovarietal stands, geitonogamy may prevail. In contrast, where a large diversity of landraces is planted, outcrossing should predominate.

In fact, strictly monovarietal stands are rare in Gabon (although I observed some exceptions among the Teke, in south-eastern Gabon, who often plant entire fields with only one landrace; Delêtre 2004). Like Aguaruna (Boster 1984b), Palikur (Pujol *et al.* 2005b) and Wayãpi (Duputié *et al.* 2009b) Amerindians, farmers in Gabon grow a mixture of manioc landraces in their farms (five on average), which they usually arrange in monovarietal patches. While outcrossing is favoured on the edges, crosses between clonemates are dominant inside the patches (Pujol *et al.* 2005b), resulting in highly skewed distribution of the levels of heterozygosity among volunteers.

[173] Pollination that occurs between flowers on the same plant, or pollination that occurs from flower to flower on different ramets of the same clone.

Selfing in manioc is associated with strong inbreeding depression (Kawano *et al.* 1978, Pujol & McKey 2006). In French Guiana, Pujol *et al.* (2005b) showed that the Palikur Amerindians exert conscious or unconscious, size-dependent selection on volunteer seedlings, resulting in a positive correlation between the probability of survival of seedlings with their size, which in turn is positively correlated with heterozygosity. Farmers hence reduce the potential impact of incorporating partially inbred manioc volunteers on the overall agronomic quality of their landraces, by selectively weeding the most homozygous seedlings. Similar directional selection was also demonstrated among the Wayãpi in French Guiana (Duputié *et al.* 2009b). In Gabon, many farmers adopted an intermediate behaviour towards manioc seedlings. Rather than discarding all volunteers (like the Ntumu or the Tsogho) or leaving them all (like the Myènè), farmers only partially weeded their farms ("thinning out"), targeting in priority the smaller volunteers, and leaving those which had already developed to a large size.

### 3.3.3. Hybridization with wild relatives

Hybridization between crops and their wild relatives is considered a major evolutionary event (Ellstrand *et al.* 1999), and one important mechanism that contributed to the secondary diversification of several crops outside their original area of domestication (Pickersgill 1998). Few barriers limit interspecific gene flows in *Manihot* (Rogers & Appan 1973, Jennings 1995), and natural hybridization is documented between the domesticated crop and a wild relative[174] in French Guiana (Duputié *et al.* 2007).

Since manioc was introduced into Africa relatively recently, the question of the contribution of the wild reservoir to the crop's genetic pool could be thought to be irrelevant in the African context[175]. In fact, the possibility of hybridization cannot be completely ruled out. In 1892, the colonial authorities have introduced another species of the Manihot genus, *M. glaziovii* Muell. Arg. (Euphorbiaceae), the Ceara rubber tree, in Congo, and later in 1895 in Guinea and Côte d'Ivoire (Lefèvre & Kouakou 1987), in an attempt to develop rubber production (Jones 1959). The experiment failed, but *M. glaziovii* is now naturalized in Africa (Halsey *et al.* 2008).

[174] With an uncertainty, however, as to whether the wild relative is *M. esculenta* sbsp. *flabellifolia*, or *M. pruinosa* Pohl. (Duputié *et al.* 2007).

[175] Interspecific hybridization with several other species (*e.g.*, *M. catingae*, and *M. dichotoma*) has been used in modern plant breeding of new manioc varieties in Africa (Ford-Lloyd & Jackson 1986, Smartt & Simmonds 1995).

The "tree manioc" is also widespread in Gabon, and locally known under a variety of names (**oguma mi ndãmbo** in Myènè [B.11a], **gegõngo sa ndãmbo** in Tsogho [B.31], **gigõngu gi ndãmbu** in Ghisir [B.41], **mbõng-ndama** in Fang [A.75], **diyaga di ndãmbu** in Lumbu [B.44]; Raponda-Walker & Sillans 1961). In Libreville, *M. glaziovii* is grown for its leaves, which are used for the preparation of various dishes (pers. obs.). In many villages, *M. glaziovii* was grown as garden hedgerows.

Sympatry of manioc and Ceara rubber could have favoured hybridization between the two species. Spontaneous hybrids of *M. esculenta* and *M. glaziovii* were reported by Cours (1951) in Madagascar and by Lefèvre and Charrier (1993) in Côte d'Ivoire. In Libreville, I observed manioc leaves that have the morphological characteristics of *M. esculenta* x *M. glaziovii* hybrids (see Lefèvre & Kouakou 1987).

The specific contribution of *M. glaziovii* to the genetic diversity of African manioc has not been investigated (Halsey *et al.* 2008). Male sterility in hybrids seems to limit the possibility of introgression of manioc (Lefèvre & Kouakou 1987), but there is, however, genetic evidence that some African cultivars are descendants of natural hybrids of manioc with *M. glaziovii* (Beeching *et al.* 1993). Incorporation could have occurred when, on a former rubber plantation, farmers opened a new manioc farm, triggering the germination of seeds from *M. glaziovii*, and favouring interspecific crosses.

## 3.4. Manioc soil seed banks, reservoir of genetic diversity

Manioc seeds can remain dormant for several decades (up to 50 years; Elias 2000). Manioc seeds from previous cycles of cultivation accumulate in the soil, constituting large seed banks ❹ that can be 'solicited' when the parcels are cleared again (see Pujol *et al.* 2007). Dormancy is broken when the soil temperature rises after forest is cleared and slashed vegetation is burned (Elias & McKey 2000, Pujol *et al.* 2002, Pujol & McKey 2006). Burning enhances germination, and seedlings usually appear within the two weeks that follow burning (Elias & McKey 2000, Pujol *et al.* 2002).

Volunteers were very common in Gabon, and with the exception of the Teke [B.71], all the farmers I interviewed had observed volunteers in their farms. Seedling densities were quite variable across farming systems, and much dependent on fallow systems and periodicity of farming cycles, but overall, densities were high, ranging from 0.7 volunteers x $m^{-2}$ in Mandilou to 3.0 volunteers x $m^{-2}$ in Mbong-Ete.

By preserving alleles and genotypes, soil seed banks preserve the memory of previous farming cycles (Pujol *et al.* 2007), and delay genetic erosion (Satterthwaite *et al.* 2007). Seedlings therefore act as 'time-capsules', occasionally releasing alleles that otherwise would have been definitively lost (Vitalis *et al.* 2004, Pujol *et al.* 2007).

In Odjouma, one rare allele, $SSR169_{109}$, was associated with the only remnant of an old sweet landrace, *Õndzalapaki*, which, my informants said, used to be very popular before it was superseded by '*Kaioio*', now grown by 45% of farmers as their only sweet landrace (Delêtre 2004, Delêtre & McKey submitted). A comparison of the allelic composition of three populations of manioc seedlings ($F_2$, $R_1$, $U_3$) with that of the landraces grown in the village revealed that many copies of this rare allele had been safeguarded in seed banks, and $SSR169_{109}$ was detected in all three populations.

Manioc seeds have played the role of 'backup' genetic diversity several times in Africa, in particular in countries where the prevalence of the most severe strains of the Cassava Mosaic Virus (CMV) disease is high. Farmers 'rescued' their landraces after drastic losses (Otim-Nape *et al.* 2001), by making cuttings from virus-free seedlings (Jennings 1963, 1970, Fregene *et al.* 2003, Gibson *et al.* 2000, Mkumbira *et al.* 2003, Kizito *et al.* 2005). Because the allelic composition of seedlings may reflect earlier stages of the system, the recruitment of seedlings may also permit a delayed transfer of alleles (Pujol *et al.* 2007). Such a mechanism, combined with the extremely high densities of manioc volunteers in Ntumu farms, has probably contributed to slow the loss of allelic diversity in Mbong-Ete (see Chapter V), even if in the case of the Ntumu, the recruitment of volunteers was not deliberate. In Odimba, the incorporation of manioc seedlings will help farmers to restore the allelic diversity lost after landraces were replaced by a limited choice of clones.

## 3.5. Natural and artificial selection on seed germination

Naturally, some selection is exerted on manioc seeds ❺, and only about 30% of manioc seeds germinate (Raffaillac & Second 2001). The environment created by farmers in their fields creates additional pressures on manioc seeds, which may either contribute to increase or to lower germination rates. Although Pujol *et al.* (2007) found no significant trend to lower densities of manioc volunteers with increasing fallow length, Duputié *et al.* (2009b) observed a significant negative effect of increasing fallow length on number of seedlings, suggesting that in long fallow systems, seed mortality may be more severe than where the fallow period is shortened.

### 3.5.1. The role of environmental factors

Variation in land management is an important parameter that greatly influences ecological opportunities for manioc seeds to germinate. In the same way that they constrain farmers' opportunity to learn about manioc volunteers, farming systems, through the heterogeneities they generate in the incidence of seedlings, can also create *in situ* dynamics of genetic diversity that may affect landraces differently.

The study I conducted in 2004 among the Teke [B.71] in Odjouma gives a unique example of how ecological differences between two different farming systems, one in forest, the other in savannah, increase the opportunities for assimilation of recombinant genotypes in the former, while reducing them in the latter, generating divergent microevolutionary dynamics in Teke manioc landraces, and leading to differences in genetic structure between landraces grown in savannah and those grown in forest.

*A bitter-sweet manioc symphony*

As in many parts of Africa (Chiwona-Karltun *et al.* 1998, Mkumbira *et al.* 2003), Teke farmers consider sweet and bitter manioc to be two distinct crops. The Teke however also categorize manioc landraces along another dimension, distinguishing those typical of forest, mainly bitter landraces, and those typical of savannah, most of which are sweet landraces. Farming systems based on savannah-forest ecotones are quite common in Africa (Blanc-Pamard 1978, Richards 1985, Fresco 1986) but this segregation of bitter and sweet manioc in two specifically allocated, spatially and ecologically distinct areas is among the most unusual characteristic features of Teke agriculture.

In savannah, farmers avoid plots that have already been cultivated. Lower intensity of land use results in lower density of soil seed banks, making volunteer seedlings rare in savannah. In contrast, forest patches are of limited availability, and restricted in size. Farmers therefore have adopted shorter fallow periods of five to ten years, and regularly re-clear some of their old plots. This difference in fallow system between savannah and forest has however important consequences for manioc volunteer seedlings. Higher numbers of volunteer seedlings were found in forest farms, while in savannah farms, seedlings were extremely rare.

An analysis of the genetic structure of manioc landraces in Odjouma demonstrated that the Teke farming system, by creating divergent evolutionary forces and maintaining two sets of landraces in an artificial situation of allopatry, creates contrasted dynamics of genetic diversity in the two pools of landraces (Delêtre & McKey submitted). Lower

incidence of manioc volunteers in savannah farms reduces considerably the probability that manioc seedlings are assimilated into local 'savannah' landraces, and over time, the lack of mechanisms such as the incorporation of seedlings to compensate for the regular loss of genotypes associated with the selection of planting material led to a narrowing of the genetic base of savannah landraces (sweet manioc), most of which were monoclonal. In contrast, in forest farms, the regular incorporation of recombinant material through the (mainly) accidental incorporation of manioc volunteers maintained, possibly even increased, the genetic diversity of landraces grown exclusively in forest, all of which were polyclonal.

### 3.5.2. Weeding practices

Sometimes, the farming system—particularly the crops sequence—also imposes weeding pressures ❻ on manioc volunteers. Manioc is capable of thriving on soils too poor for other crops to establish (Jones 1959). However, on rich soils, s such as those of forest plots that are cleared for the first time, above-ground parts (stem and leaves) develop at the expense of the roots (Jones 1959).

*The peanut-manioc antagonism*

In Gabon, farmers usually grow plantains for one farming season before they plant manioc (*e.g.*, the Ntumu [A.75a] in Mbong-Ete, the Ghisir [B.41] in Mandilou), and always associate other crops (generally maize) with manioc. On plots which were left fallow for a short period of time, farmers always sow peanuts first, and then only intercrop it with manioc (*e.g.*, the Ntumu [A.75a] in Mbong-Ete, the Tsogho [B.31] in Douani, and the Ndzabi [B.52] in Makoula). Manioc, therefore, is never at the start of the crop succession, and weeding always precedes manioc planting.

Manioc volunteers develop during the first few weeks following burning of the new farms (Elias & McKey 2000, Pujol *et al.* 2002), and therefore appear when they are least wanted. In Mbong-Ete and Makoula, manioc volunteers were weeded out because they competed with peanuts and could hinder their development. Hence, weeding pressures on manioc volunteers tended to be harsher wherever manioc was intercropped with peanuts. Meanwhile, because peanut cultivation requires a perfectly clean soil, farmers generally grow peanuts in farms which have been left fallow for two or three years only, and where trees are still small, hence easier to clear out.

By reducing intervening fallows between cultivation cycles, farmers potentially reduce natural mortality among seed (although this will need to be tested, data are suggestive, as shown by Duputié *et al.* 2009b). Hence, paradoxically, while peanut cultivation, prior to intercropping with manioc, imposes a stronger human selection of manioc volunteers, it possibly reduces, conversely, natural selection on germination. With the increasing number of volunteers germinating after burning (suggested by the huge densities of manioc seedlings found in Ntumu farms), the proportion of volunteers that will escape farmers 'sieve' of weeding, will proportionally increase, thereby increasing the chance for accidental incorporation of manioc self-sown seedlings. Consistently, the levels of genotypic diversity found in Ntumu and Tsogho manioc farms did not bear out the reported behaviours of farmers, who stated they systematically discarded manioc volunteers. This confirms that a substantial proportion of seedlings are accidentally incorporated. I suggested, for the Fang, that the discontinuation of weeding beyond peanuts harvest and delayed harvesting of manioc may increase the 'risk' of such unconscious recruitment of recombinant plants.

### 3.5.3. Appearance and performance: the uneasy connection

Although the Ntumu were an exception to the rule, all farmers I interviewed enjoyed experimenting with novelty and eagerly adopted new landraces. New landraces were frequently acquired from relatives and neighbours, or from other villages. They showed, however, little interest in manioc volunteer seedlings, and paid no heed to this potential source of diversity.

*The paradox of diversity in African manioc farms*

Part of the answer to this paradox lies in the folk reasoning beyond farmers' experimental approach to diversity. The segregation of bitter and sweet manioc I documented among the Teke is not arbitrary, but reflects farmers' empirical observation and assessment of the agronomic performance of each individual landrace in a changing and heterogeneous environment. These *in situ* experimentations are part of a continuous learning process that aims at identifying, for every landrace, its 'norm of reaction', that is, the range of variation in cultivation conditions it can tolerate, and the effect of these variations on yield.

For farmers, the planting of a new farm is the occasion to translate into actions the conclusions of their previous observations, and the varietal composition of a farm may change from one year to the other, with some landraces being favoured and planted in higher densities than other. In most villages I surveyed, a small proportion only of the total diversity present at the village level accounted for the biggest part of the production of manioc. This learning process however implies that a landrace conforms to its ideotype, that is, a mental picture that associates a set of morphological characteristics to a pattern of agronomic behaviours and organoleptic properties, thereby limiting $V_P$ to deduce $V_{GxE}$. Sexual reproduction stirs together the genetic pool of the collection of landraces found within a farm, and produces new combinations of alleles, thereby adding to genetic diversity. However, sexual reproduction also allows the segregation of characters, and breaks up previous combinations of phenotypic characters which farmers may have wanted to preserve. Studies have shown that several morphological traits in manioc, such as leaf width and shape, leaf vein colour, root parenchyma colour and stem colour—all playing an important part in the identification of manioc landraces [*e.g.*, among Aguaruna farmers in Peru (Boster 1985b), the Caiçara farmers in Brazil (Sambatti *et al.* 2001), and farmers in Uganda (Kizito *et al.* 2007)]—have a Mendelian inheritance (see Sambatti *et al.* 2001). Other characteristics, such as bitterness, appear also to have a certain degree of 'freedom' and to be only partly inheritable (see Chapter IV).

Farmers aim at keeping their landraces within consensual, well-defined morphological schemes, which is conditional for preserving the efficacy of folk taxonomical systems. In Malawi, Mkumbira *et al.* (2003) demonstrated, from genetic evidence, that this need to maintain 'perceptual distinctiveness' (Boster 1985) between landraces leads to a rather strict matching between folk nomenclature and genotypic identity, and to a narrowing of the genetic basis of most common landraces.

In Gabon, farmers' behaviours towards manioc volunteers reflected a general concern that volunteers threaten the ideotype that farmers want to maintain for each of their landraces, as a way to maintain the artificial association between performance and appearance permitted by clonal propagation, and without which there is no way for farmers to learn about the ecology of their manioc landraces. Farmers' reluctance to use volunteers therefore partly stems from a necessity to preserve the function of landraces as the "minimum unit of perception and management of diversity" (Emperaire *et al.* 2003).

### 3.5.4. Directional or cognitive selection

There are two directions in which farmers can orientate this ideotypic selection. One that systematically rejects 'off-type' plants and leads farmers to reject manioc volunteers because 1) they do not look like any known landrace (selection for "perceptual indistinctiveness" ❼, *sensu* Manu-Aduening *et al.* 2005), as in the case of Teke farmers; or 2) because the volunteers, although they display characters of a known landrace, are unreliable for other characteristics of interest to farmers, such as bitterness, as in the case of the Tsogho. This may be considered as a form of directional (that is, yield based) counter-selection, although it does not stem on an empirical evaluation, through trials, of the properties of the seedlings, but on the belief of volunteers having such or such characteristics, *e.g.*, low yield (the majority of farmers in Gabon, but also in Ghana; see Manu-Aduening *et al.* 2005) or high levels of cyanides.

The second way ideotypic selection can go is a selection for "perceptual distinctiveness" (Boster 1985b), which will, conversely, channel the selective incorporation of volunteers on the basis of a morphological dissimilarity with other existing landraces ❽. Those which differ will be multiplied and given a name, thereby adding to the varietal diversity at the community level. This is the form of cognitive selection ❾ (*sensu* Shigeta 1996) I described among the Myènè in Odimba and Nombedouma (Chapter III). Although other farmers also often acknowledged the possibility that volunteers display unusual morphological characteristics, only the Myènè valorised and made use of this diversity.

### 3.5.5. Taming manioc: the role of naming systems

The importance of the Myènè naming system goes however beyond the simple act of creation of a new landrace by giving it a name, as applying in a label. Naming self-sown seedlings is a highly cultural process (Salick *et al.* 1997, Caillon & Degeorges 2007), which engages the intimate beliefs of farmers about the origin of the volunteers. It entails a degree of re-appropriation of the plant that manioc farming societies have rarely achieved in Africa.

Ritual and mythical life surrounding manioc cultivation similar to that found in Amazonia (Salick *et al.* 1997, Rival 2001, Heckler & Zent 2008) does not exist in Africa, , whereas other vegetatively propagated crops, in particular bananas, play a central role in the religious life of many African societies, particularly in Gabon (Perrois 1968, Rossel 1998). Until now, the Myènè are the only documented case of a truly cultural indigenous form of manioc 'breeding' in Africa.

In the other villages I surveyed (such as in Imbong, Makoula, Mopia, and Odjouma), those farmers who did not discard volunteers rarely made use of the stems after harvest. They were not receptive to new morphotypes that appear in their farms, and which they could not categorize into an already named landrace. In these villages, farmers believed volunteers to be "safe" as long as the plants could be ascribed to a landrace they knew. Hence, the corollary of ideotypic selection, which maintains perceptual distinctiveness among landraces, is a selection for perceptual indistinctiveness among manioc volunteers. Ideotypic selection therefore channels the selective incorporation of recombinant genotypes, driving selection against unfamiliar phenotypes while favouring in return those perceptually indistinguishable from local landraces.

In French Guiana, Duputié *et al.* (2009b) have shown that this mechanism allows Wayãpi Amerindians to maintain high levels of diversity within their landraces, while also maintaining high levels of genetic differentiation between their landraces. The authors also showed that perceptual selection of volunteers was also correlated with higher average relatedness between manioc seedlings and the landraces they were assigned to. In essence, this means that this form of perceptual selection also ensures the maintenance of a certain genetic 'integrity' within landraces.

In Gabon, as probably in many other parts of Africa, a similar mechanism may have played a central role in facilitating the incorporation of manioc volunteers into the stock of propagules. However, how much this mechanism contributes to increase intravarietal diversity hinges, ultimately, on farmers' folk knowledge about manioc self-sown seedlings, and how cognizant they are of the real origin of manioc volunteers.

Because the assimilation of products of sexual recombination to traditional landraces compromises the pertinence of those artificial associations between appearance and performance, farmers rejected in mass manioc volunteers. But this entails that farmers are aware of the sexual origin of volunteers, and of the differences that may exist between them and their closest morphologically resembling landrace.

Perceptual selection at an early stage in the seedlings' life is expected if, as in the case of the Teke, farmers ignore the real nature of seedlings, and believe them to be resurgence of cuttings, therefore to be 'safe'. Implicitly, farmers associate clonal propagation with a guarantee of stable characters and reliable behaviour, explaining why a larger proportion of farmers incorporated volunteers when they thought them to originate from stem cuttings (Figure 6.2). This results in volunteers being selected in a more arbitrary way, and farmers rarely assessed the agronomic quality of volunteers, which would require leaving them to first reach maturity, and evaluating them only after a first cycle of clonal propagation, as the Amerindians do (Elias *et al.* 2000a, Duputié *et al.* 2009b).

This intermediate step, however, does not exist in the chains of behaviours I observed in Gabon. When they "experimented" with volunteers, farmers never extended the evaluation beyond harvest, and did not attempt to make stem cuttings of manioc volunteers. In Mbong-Ete, Douani and Odjouma, Ntumu [A.75a], Tsogho [B.31], and Teke [B.71] farmers keep their landraces "true-to-type" by exerting stringent ideotypic selection on planting material, discarding variant morphotypes, and propagating only individuals matching specific morphological criteria and conforming to their ideotype of the landrace. As several authors have observed, such stern selection often results in a reduction in the number of genotypes within a given landrace, relative to its popularity, *i.e.*, its frequency amongst farmers. In Malawi, Mkumbira *et al.* (2003) showed that the number of distinct MLGs tended to diminish among the most common cultivars. In Gabon, I found however no clear relation between the popularity of landraces and their genotypic diversity, and found in fact most landraces to be polyclonal.

### 3.5.6. The role of accidental incorporations of volunteers

As reflected by the levels of genotypic diversity I found in Douani and Mbong-Ete, accidental incorporation of manioc volunteers seems to be happening at unexpectedly high frequency, even in those farming systems which impose strong weeding pressures (*e.g.*, that of the Ntumu in Mbong-Ete; see Chapter V).

To the practiced eye, manioc volunteers can be distinguished in farms by the presence of cotyledons on young seedlings, and by the frequent absence of ramification and shorter internodes at the base of the stem in older plants (Pujol *et al.* 2005b). While Amerindian farmers use these criteria to recognize self-sown manioc plants in their farms, I found that farmers in Gabon were generally unable to differentiate seedlings from cuttings once the plant reached maturity. Farmers identified volunteers as 'outsiders', literally, as they grew

outside the mounds prepared for planting manioc (*e.g.*, the Teke, in Delêtre 2004) and because they develop a single stem, which contrasts with the multiple stems that develop from cuttings (*e.g.*, the Fang in Mbong-Ete, in Chapter V). In a mature manioc stand, however, it becomes difficult to distinguish volunteers within the maze of manioc stems and weeds that invade slowly the parcel (see Sambatti *et al.* 2001).

The presence of a tap-root instead of the usual lateral roots which develop from cuttings, and the absence of a cutting at all at the base of the plant, are two criteria which should allow farmers to discard manioc volunteers when they harvest roots or when they select fresh stems for planting the next set of farms. However, the method used to harvest plants (stems and/or roots) will determine how many volunteer plants will escape this last step of counter-selection.

Where manioc is grown mostly for subsistence (as in Douani), plants are harvested on a daily or weekly basis. Farmers uproot the plants they need, collect the roots, and replant the cuttings immediately afterwards. If a volunteer is—quite literally—uncovered, it will be discarded. In market-oriented farming systems, such as that of the Ntumu in Mbong-Ete, manioc stem cuttings are harvested in bulk, to supply the large amount of cuttings required for planting the new sets of farms. Fresh stems are usually sourced from older stands, which stopped producing, and cuttings are taken from unharvested plants (as is the case of the Cashinahua farmers in Peru; see McKey & Beckerman 1993). Manioc volunteers, inconspicuous if they are morphologically indistinguishable from that of a common landrace, may be incorporated by genuine mistake (see also Sambatti *et al.* 2001).

## 3.6. Exchanging clones

Because they considered manioc volunteers either ‘harmful’, ‘deceitful’ or simply ‘worthless’, farmers in Gabon favoured material of known origin over the use of manioc volunteers to source germplasm. Consistently, exchanges of cuttings represented 96% of the source of the manioc landraces grown by farmers I interviewed[176] (Chapter II). Migration of clones ❿ therefore represented the chief mechanism through which farmers (consciously) increased manioc diversity at the local level.

[176] The 4% being represented exclusively by the Myènè.

To get new landraces, women borrowed cuttings from neighbours and relatives, or from other villages (see Chapter II). Multiple introductions of planting material from various origins, through these exchanges, favour the concentration of diversity at a small geographic scale, and the constitution of passive hotspots. In some villages, the social valuation of diversity, through the prestige and power it gives to farmers who hold large numbers of landraces (Elias *et al.* 2000b, Heckler & Zent 2008), can also result in a local concentration of landraces. With the example of yellow varieties in Douani (Chapter IV), I have shown however that exchanges can also artificially increase diversity, by multiplying cases of synonymy.

Given the importance of the flow of germplasm between communities, the inventory of named landraces cannot alone give an appropriate estimation of the regional diversity, and an analysis of the underlying genetic diversity is indispensable. A neighbour-joining tree based on Cavalli-Sforza and Edwards (CSE) chord genetic distance, constructed from a sample of 168 (74 sweet and 94 bitter) named accessions (Appendix C4), showed that about one third of all the names I have recorded in Gabon (406 in total, listed in Appendix B4) may be, in fact, synonymous.

In Gabon, about two-thirds of the exchanges of germplasm occur within the family circle. Vertical transmission was predominant in all but one village (see Chapter II). By documenting farmers' kinship networks, I circumvented the possible bias the predominance of germplasm exchanges between kins could have had on my estimation of the consistency of folk taxonomy systems. However, it also allowed me to unveil the particular importance the modes of transmission of manioc landraces can have on the local dynamics of genetic diversity.

The unusual system of transmission of manioc landraces among the Ntumu (Chapter V) highlights the importance of taking into consideration kinship systems and the modes of transmission of manioc landraces in interpreting the structure of genetic diversity at the local [177] level. Whether landraces are transmitted vertically (mother to daughter), diagonally (farmer to affine, *i.e.*, in the case of the Ntumu, mother-in-law to daughter-in-law) or horizontally (farmer to peer) has a direct impact on manioc genetic diversity, and may favour or limit the inwards migration of new genotypes.

[177] Or, in the case of the Ntumu in Gabon, at the regional level even.

Keeping in mind that women are the carrier of folk taxonomical knowledge and the main vector of diffusion of manioc landraces (see Chernela 1987, Emperaire & Peroni 2007), another important factor to consider is therefore the rule of residence. Whether virilocality or uxorilocality is the rule will constrain the movement of women from outside the village into the community, and therefore the migration of new landraces (or new clones) into the village. In Odjouma, exogamy and virilocality have favoured the migration of several new landraces from the Congo, and led to the accretion of more than 60 different varieties in the village (Delêtre 2004, Delêtre & McKey submitted). In Mbong-Ete, conversely, affinal transmission opposes the migration of clones inside the community, which functions in complete autarchy and, as a result, as a closed system for manioc genetic diversity.

This last example shows that the finest degree of analysis of the dynamics of crop genetic diversity can be achieved by using the appropriate tools. The cultural diversity surrounding manioc cultivation in Gabon underlines that even for a question of evolutionary biology, obtaining the answer may require combining different methods and looking at the question from a variety of points of view, accruing from disciplines as varied as genetics, anthropology, or history.

In the same way that Haudricourt (1964) stressed the input of ethnobotany to the general understanding of genetic patterns of diversity, genetics, in return, can help solving problems of an ethnographic nature, and vice versa. Because manioc is mostly propagated by means of stem cuttings, farmers, when they exchange landraces, exchange clones, which can be used as genetic 'markers' to trace back the past history of manioc diffusion in Gabon. Studying the spatial patterns of manioc genetic diversity in Gabon can thus give insights into the historical trajectories of manioc in Gabon, and the sequence of its adoption by the people. Considering historical factors, in turn, proved necessary to understand the grounds of farmers' valuation of manioc diversity.

# 4. Plants affect people

In this chapter, I have synthesized my findings from a series of village-level studies of local manioc farming systems in Gabon, and I have highlighted several of the mechanisms through which manioc diversity is amplified in African manioc agricultural settings. They can be summed up as follows, in decreasing order of importance:

1. the **exchange of clones**, within and among communities, leading to the accumulation of diversity at the local level (*e.g.*, the Teke, in Delêtre 2004);
2. the **accidental incorporation of volunteers**, which happens mostly as a result of the ecological opportunities created by the farming system, in particular the turn-over of land use, which in turn depends on demographic pressures. In essence, the case I documented among the Ntumu (Chapter V) shows that where pressure on land increases, the density of soil seed bank increases in proportion to the periodicity of land turn-over, and a small yet substantial percentage of volunteers always escape farmers' attention, resulting, eventually, in the incorporation of recombinant plants into the stock of propagules;
3. the **fostering of volunteers**, without the intention of propagating them, but increasing nevertheless the opportunities for unconscious recruitment of volunteers after harvest (*e.g.*, the Ghisir in Chapter IV);
4. and finally, the **cognitive selection** of self-sown recombinant plants (*e.g.*, the Myènè in Chapter III).

Local 'seed' production systems, that is, the autogenous and local forms of breeding, are essential for *in situ* conservation of crop diversity. A better understanding of the grounds of farmers' valuation of diversity and for selecting particular landraces, but also a better evaluation of the respective contribution of the different mechanisms I presented here to the general dynamics of genetic diversity of manioc, are necessary for developing participatory or collaborative plant breeding strategies that aim at reconciling the local (Almekinders *et al.* 1994) and formal plant breeding systems (Witcombe *et al.* 1996), and avoiding genetic erosion through cases of seed replacement (*e.g.*, de Barbentane *et al.* 2001, Sperling & Longley 2002). It also entails understanding the rationales behind farmers' behaviours pertaining to the management of manioc volunteers, and accompanying any proposed changes with measures to protect local diversity (Cleveland *et al.* 2000).

## 4.1. The iron collar of past

As I have illustrated in the previous chapters, the diversity of farming practices in Gabon reflects, to a large extent, the evolution of the historical and political context of Gabon between the 18th and 20th centuries.

In northern Gabon, the organisation of the farming system, its deep integration within a market system, and even the patterns of manioc diversity at the village and the regional scale are all the sequels of the great famine of the 1920s and of the successive policies adopted by the colonial authorities to face food shortages and stabilize the region. In another Ntumu village, Nkongmeyos[178], in south-western Cameroon, Carrière (1999) described a rather different farming system[179]. The most striking and most revealing difference between the Ntumu of northern Gabon and the Ntumu of southern Cameroon, however, is the status that manioc has achieved as a crop. In Mbong-Ete, manioc is the main staple and the main source of income. In Nkongmeyos, manioc comes second after squashes (*Cucumeropsis mannii* Naudin), while cacao brings most of the revenue and manioc is grown solely for subsistence.

After the collapse in the 1980s of the market for cacao, the Woleu-Ntem redeveloped its economy to food agriculture (plantains, peanuts, manioc, yams) to supply urban areas, in particular Libreville and Port-Gentil, exerting further pressure on local farming. Since September 2008, the Gabonese government initiated in Oyem an ambitious project[180] to develop and modernize agriculture in the Woleu-Ntem[181]. With the help of IFAD (International Fund for Agricultural Development), the Gabonese government invested 3 billion FCFA to boost production in the region and reduce the country's food import bill[182]. The project plans on developing nurseries for peanuts, plantains and manioc, and promoting the creation and organisation of local farming cooperatives, while providing the facilities for the transformation and commercialization of farm products.

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[178] About 200km west of Mbong-Ete.

[179] Carrière (1999) identified six different types of farms: **esep ngwan**, dedicated to squashes; **asan**, first planted with squashes then with plantains, macabo and manioc; **afup owono**, where peanuts are the main crop; **kunu** farms, where a large variety of crops are planted following peanuts; **afup bikwan**, where plantains succeed to squashes or peanuts; and finally, **afup olis**, the rice farms, which have been completely abandoned in Mbong-Ete.

[180] PDAR ("Projet de Développement Agricole et Rural")

[181] "L'Union", 6 November 2007.

[182] About 60% of the country's agricultural needs are imported (FAO 2008).

Given the slow evolution of named (and genetic) diversity in the Woleu-Ntem (Chapter V), the strategy of the Gabonese government to develop agriculture in the region may contribute to increasing both varietal and allelic diversity at the regional level. How the proposed modernization of agriculture in Woleu-Ntem will affect manioc diversity at the regional scale will however strongly depend on the amount of diversity the project will inject in local farming systems, and on the measures that will accompany the introduction of these new cultivars. The new varieties may not succeed in spreading among farmers, as in the case of '*Dame Jaune*'. Or, if they perform better than their older competitors, they may quickly replace local landraces. Important information about the history of manioc farming in Gabon and about the movements of people may be lost along with the different genotypes of '*Adzoro*'.

Similar loss of valuable historical information is pending among the Myènè, where careless distribution of manioc cuttings could lead to the complete disappearance of the landraces that could have been associated with early introductions of manioc into Gabon. Several cases of seed replacement have been documented, and are often linked to the adoption of modern varieties to the detriment of local landraces (Brush & Meng 1998). However, the risk of detrimental "collateral" effects from the intermingling of formal seed systems with informal seed systems is multiple and complex (Caillon & Degeorges 2007), and goes beyond the sole risk of eroding genetic diversity. As I highlighted with the case of the Orungu in Odimba (Chapter III), it may directly jeopardize cultural diversity, the loss of which would be even more detrimental to the crop that the loss of the landraces (Emperaire *et al.* (1998).

Beyond the cultural significance and patrimonial importance of landraces, tempering of the formal seed system with local seed systems not only threatens to homogenize diversity at the regional or country-scale, but it also reduces the need for farmers to interact and exchange landraces, and thereby to exchange information (Boster 1986). Heckler and Zent (2008) have highlighted, in particular, the social significance of these germplasm exchanges as means of nurturing relationships with other farmers, and strengthening the social cohesion not only within the community but also with other communities. Because folk taxonomic systems rely on a shared knowledge and consensus between farmers on the names given to the different types of a crop, the risk associated with increasing the dependency of farmers on outer sources of diversity is also the loosening of social cohesion, and the disappearance, over time, of folk taxonomic knowledge, and with it, of a large part of the diversity itself.

## 4.2. Building on farmers' local expertise

Cooper and Byth (1996) have suggested that modern plant breeding strategies should move their goals from wide to specific and local adaptations, and provide farmers with a choice of cultivars tuned to their particular ecological and cultural environment. In this sense, participatory plant breeding (PPB) strategies, which build upon local expertise and consider farmers' reasons for growing diverse varieties, are more appropriate than participatory variety selection (PVS), where farmers are solely involved in the last phase of the selection process (Witcombe *et al.* 1996). The risk is that a single, higher-performing clone will spread and completely occlude pre-existing genetic variability at the local level. A better understanding of the grounds of farmers' valuation of diversity and preferences for particular types is therefore a first step to a better integration of formal and informal seed systems.

Because of their embeddedness (*i.e.*, strong temporal and cultural specificity) and contextuality, my observations on African folk knowledge about manioc volunteers cannot be used, as such, to develop such strategies outside the communities from which they were drawn. However, my study gives the methodological basis for a more comprehensive study of the determinants of farmer-plant relationship, and how they determine the interactions of farmers with the biological traits of crop plants, and affect, ultimately, the local management of on-farm diversity.

Genetic variation is the raw material for evolutionary change within populations (Frankel & Soulé 1981), and the loss of this diversity threatens the resilience of local farming systems. Given the intricate nature of the relation between cultural diversity and genetic diversity, it is clear that landraces, as much as the cultures which have produced such diversity of forms, need to be both documented and protected.

Manioc is now deeply ingrained into African traditions, but the articulation of the cultural and agricultural dimensions of manioc diversity has been largely overlooked. This neglect stems, I believe, largely from the fact that the crop is not native to Africa. Studies that focussed on agrobiodiversity have focussed mostly on crop plants in their area of domestication [on manioc in Peru (Boster 1984b, Salick *et al.* 1997) and Amazonia (Emperaire *et al.* 1998, Elias *et al.* 2000a,b, Duputié *et al.* 2009b); on common bean in Mesoamerica (Zizumbo-Villarreal *et al.* 2005); on maize in Mexico (Perales *et al.* 2003, Pressoir & Berthaud 2004, Brush & Perales 2007); on taro in Vanuatu (Caillon *et al.* 2006); on sorghum in Ethiopia (Teshome *et al.* 1997) and sub-sahelian Africa (Barnaud *et*

*al.* 2007); and on fonio (Adoukonou-Sagbadja *et al.* 2006) and yams in West Africa (Dumont *et al.* 2005, Scarcelli *et al.* 2006)], but very little, comparatively, in crop areas of introduction. This leaves substantial gaps in the general understanding of person-plant interactions and their role in shaping crop diversity. Unless we document and understand these interactions, genetic erosion is bound to follow the disappearance of local folk knowledge that built up this diversity.

## 4.3. Out of Africa

People affect plants, because plants also affect people. This study of cross-cultural variations in perception and valuation of diversity has shown that the factors that most influence levels of diversity are neither simply cultural, social, or ecological. Outside its range of origin, diversity of a crop is first and foremost influenced by the modes and vectors of its spread.

I have shown in this thesis that present patterns of diversity can be conditioned, to a large extent, by the joined history of the plant and the people. In this reciprocal interaction of the plant with the farmers, the modes of transmission of manioc in Africa have had a determinant influence that still shows in variations among populations in their valuation and use of manioc volunteers as a potential source of diversity.

Manioc in Africa is perhaps extreme as an example, as the crop was largely 'instrumentalized' by the agents of its introduction and spread in Africa. Firstly by the Portuguese during the slave trade, where manioc was used for feeding slaves; then during the colonial period, by the French, English, and Belgians, as a food security crop and means of economic control. Considering the political and economic dimensions of the processes of crop acculturation therefore seems a relevant approach when studying the diversity of crops outside their native natural and cultural environments.

In Gabon, manioc introduction had important social, cultural, and economic repercussions for populations, and these repercussions have had, in turn, important consequences for manioc farming practices and for manioc diversity at the local and regional levels. Through this process of 'cultural domestication', farmers influenced genetic diversity in their manioc populations by channelling differently the impact of sexual reproduction on the dynamics of genetic diversity of the crop populations.

I do not argue that the historical question of manioc spread in Africa has had as much an impact on present patterns of farming practices in the rest of Africa, as it had in the examples I presented in this thesis. I only advocate that much is to be gained from enlarging the study of plant-farmer interactions to other parts of Africa, and encouraging the study of cross-cultural variations with a thought for the initial circumstances of the crop's introduction.

The insertion of the comparative study of manioc farming in Africa into the historical continuum of the transformation of African agricultural systems along with the evolution of African economies during the transition from pre-colonial trade to formal colonial rule gives insights for a fuller understanding of present variations in manioc diversity in Africa.

Other important areas of Africa where similar studies could be undertaken for further investigation of the importance of historical factors in explaining current patterns of diversity could include São Tomé and Príncipe, which may have acted for over a century as a 'reservoir' of diversity and where planting material imported from Brazil was probably 'stored' before diffusing later throughout the continent. Sierra Leone and Togo would be two other interesting areas to conduct surveys. The return of freed African slaves from Brazil in the 18$^{th}$ century could have helped not only the spread of processing techniques (Jones 1959), but could also have contributed to introducing there folk knowledge about manioc volunteer seedlings learned from the Brazilians. On the East part of Africa, the coast of Mozambique, La Réunion and Mauritius could finally provide material to draw a better picture of the second wave of introduction of manioc into Africa.

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# Appendices

# Supplementary maps

# A1. Languages of Gabon

**Table A1. Classification of the languages of Gabon**, based on the revision of Guthrie's classification of Bantu languages (Guthrie 1948) as proposed by Maho (2003). The list below is not exhaustive, but includes some of the name variants found in the literature, and a list of the Pygmy groups living in Gabon.

## Zone A

| | |
|---|---|
| **A.30** | ***I. Bubi-Benga group*** |
| A.34 | Benga |
| **A.70** | ***II. Ewondo-Fang group*** |
| A.75 | Fang, Pangwe |
| A.75a | Ntumu |
| A.75b | Okak |
| A.75c | Meke, Make |
| A.75d | Atsi, Betsi |
| A.75e | Nzaman, Zaman |
| A.75f | Mveny, Mvae, Mvaï |
| **A.80** | ***III. Makaa-Njem group*** |
| A.803 | Shiwe, Ossyeba, Makina |
| A.85b | Bekwil, Bekwel, Kwele |

## Zone H

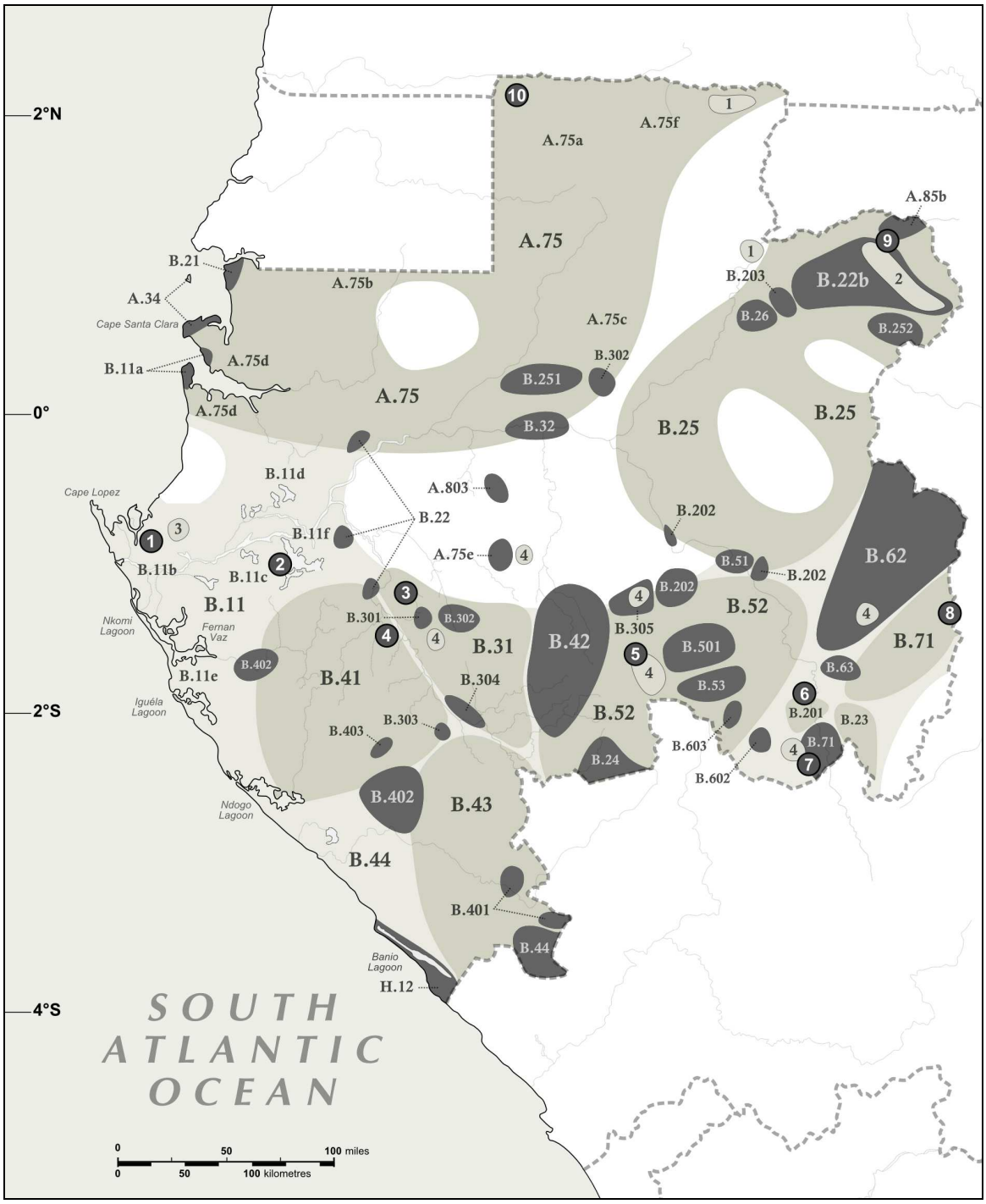
| | |
|---|---|
| **H.10** | ***IV. Kongo group*** |
| H.12 | Vili, Civili |

## Pygmies

| | | |
|---|---|---|
| **1.** | **Baka** | Around Minvoul and Bélinga |
| **2.** | **Koya** | Around Mékambo |
| **3.** | **Akoa** | Around Port-Gentil |
| **4.** | **Bongo** | Around Booué, Franceville, Lastoursville, Akiéni, Pana, and Mimongo |

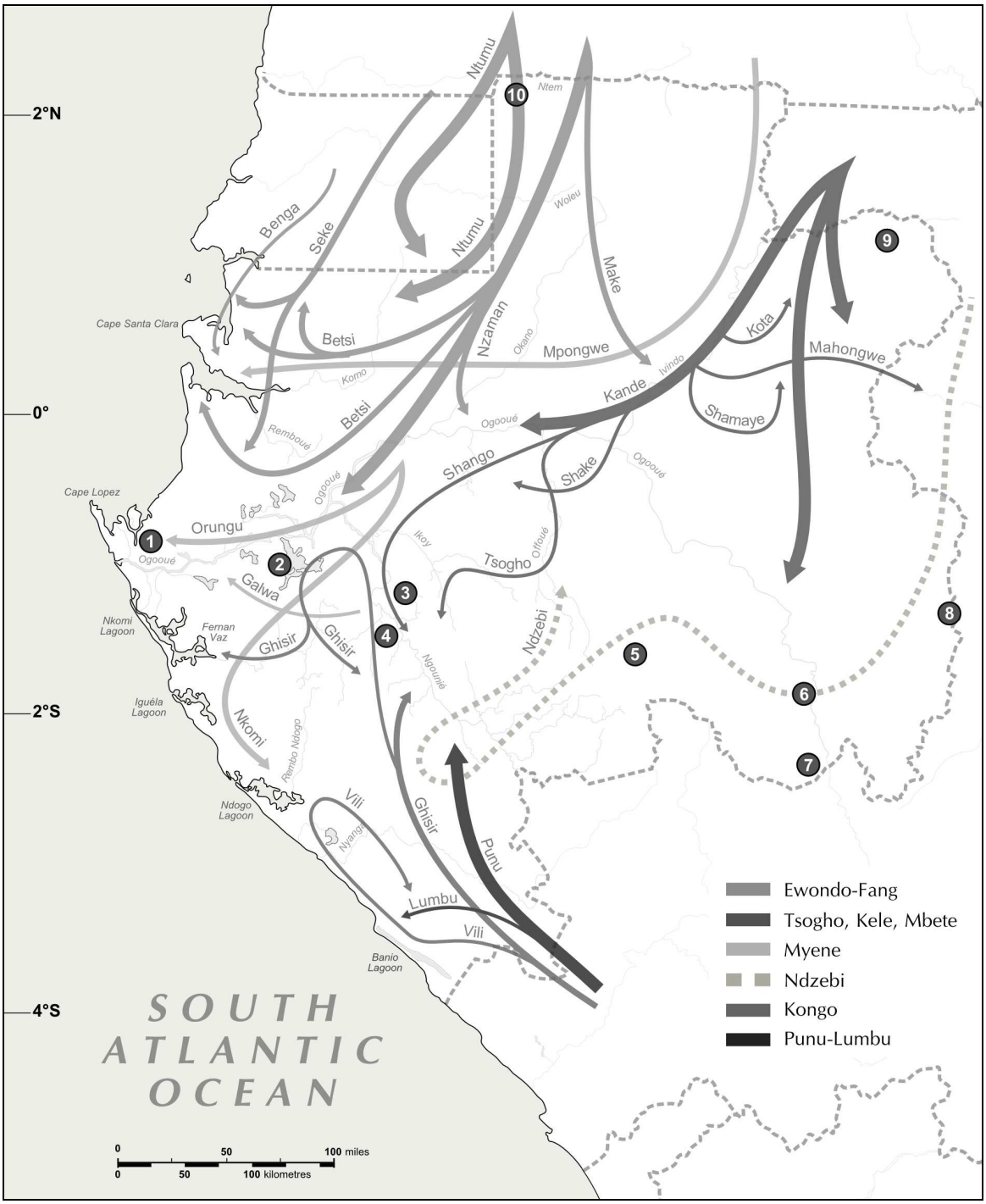
## Zone B

| | |
|---|---|
| **B.10** | ***V. Myènè group*** |
| B.11a | Mpongwe |
| B.11b | Orungu, Rongo |
| B.11c | Galwa |
| B.11d | Dyumba, Adjumba |
| B.11e | Nkomi |
| B.11f | Enenga |
| **B.20** | ***VI. Kele group*** |
| B.201 | Ndasa, Andasa |
| B.202 | Sighu, Sigu |
| B.203 | Sama, Shamaye |
| B.21 | Seki, Shekiani |
| B.22 | Kèlè |
| B.22b | Ungom, Ngom, Bongom |
| B.23 | Mbanwe |
| B.24 | Wumvu |
| B.25 | Kota |
| B.251 | Shake |
| B.252 | Mahongwe |
| **B.30** | ***VII. Tsogho group*** |
| B.301 | Via, Ivea, Eviya, Avia |
| B.302 | Himba, Simba |
| B.303 | Bongwe, Ebongwe |
| B.304 | Pinzi, Apindzi |
| B.305 | Pove, Vove, Bubi |
| B.31 | Tsogho, Ghetsogo |
| B.32 | Kande, Okande |
| **B.40** | ***VIII. Sira group*** |
| B.401 | Bwisi |
| B.402 | Varama, Barama |
| B.403 | Vunghu, Vumbu |
| B.41 | Sira, Shira, Ghisir |
| B.42 | Sangu, Shango |
| B.43 | Punu |
| B.44 | Lumbu |
| **B.50** | ***IX. Ndzebi group*** |
| B.501 | Wandzi, Wandji |
| B.51 | Duma, Adouma |
| B.52 | Nzebi, Ndzabi, Njabi |
| B.53 | Tsaangi, Tsengi |
| **B.60** | ***X. Mbete group*** |
| B.602 | Kaningi |
| B.603 | Yangho |
| B.62 | Mbaama, Mbamba |
| B.63 | Ndumu, Mindumbu |
| **B.70** | ***XI. Teke group*** |
| B.71 | Northern Teke |
| B.78 | Wumbu |



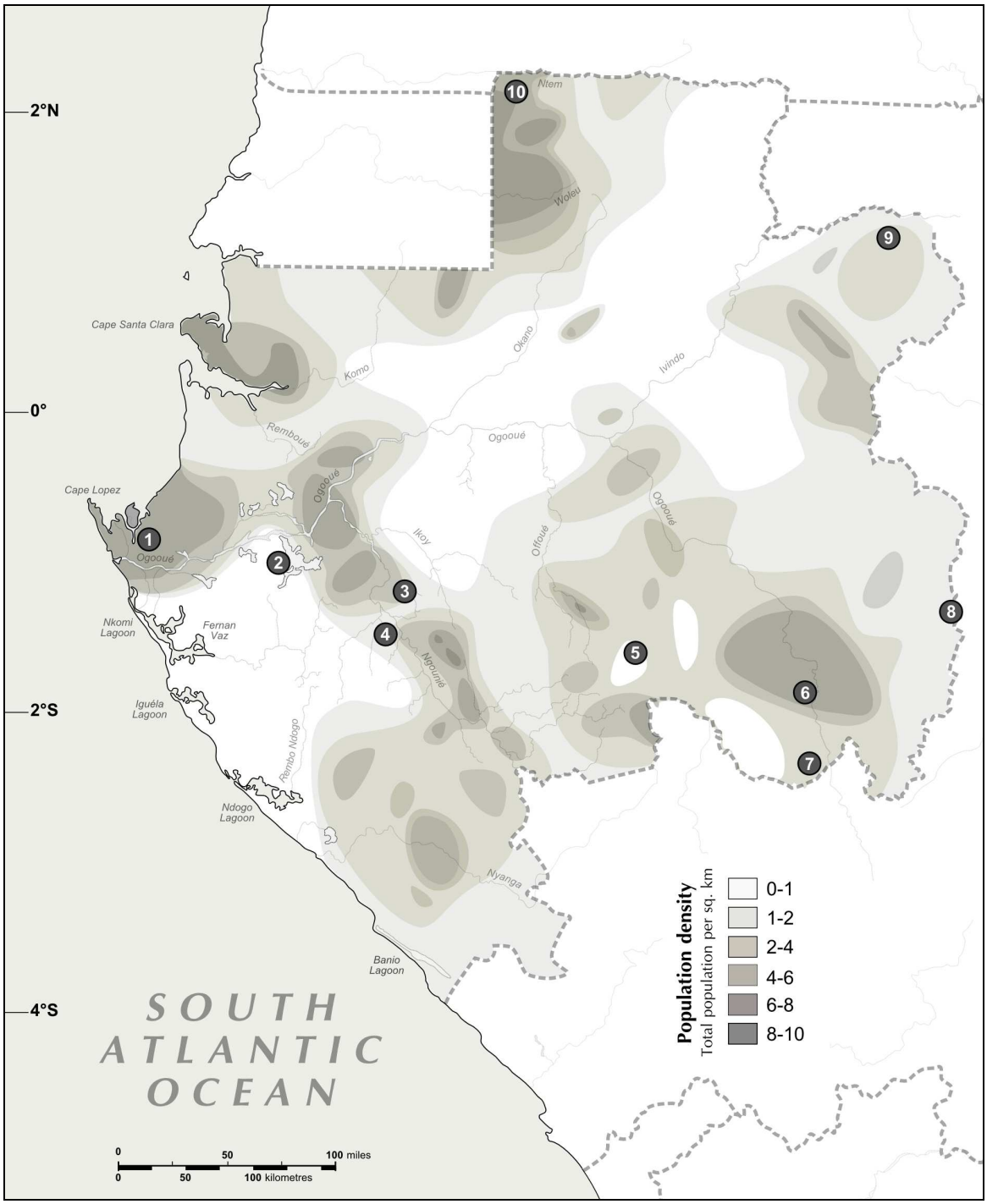

**Map A1. Distribution of languages in Gabon.** The current pattern of distribution of populations in Gabon reflects the changes which occurred with the emergence of slave trade, and later, between the 19th and early 20th century, with the establishment of factories and the nascent French colony in Gabon (see Merlet 1990, 1991, Patterson 1975, and Gray 2002). Refer to Table A1 for the names of ethnic groups and the corresponding codes. Blank areas correspond to uninhabited regions. Study sites (❶ to ❿) are reported on the map. Data from Jacquot (1978), Bahuchet (1985), and Nurse (2001).

# A2. Past migrations in Gabon



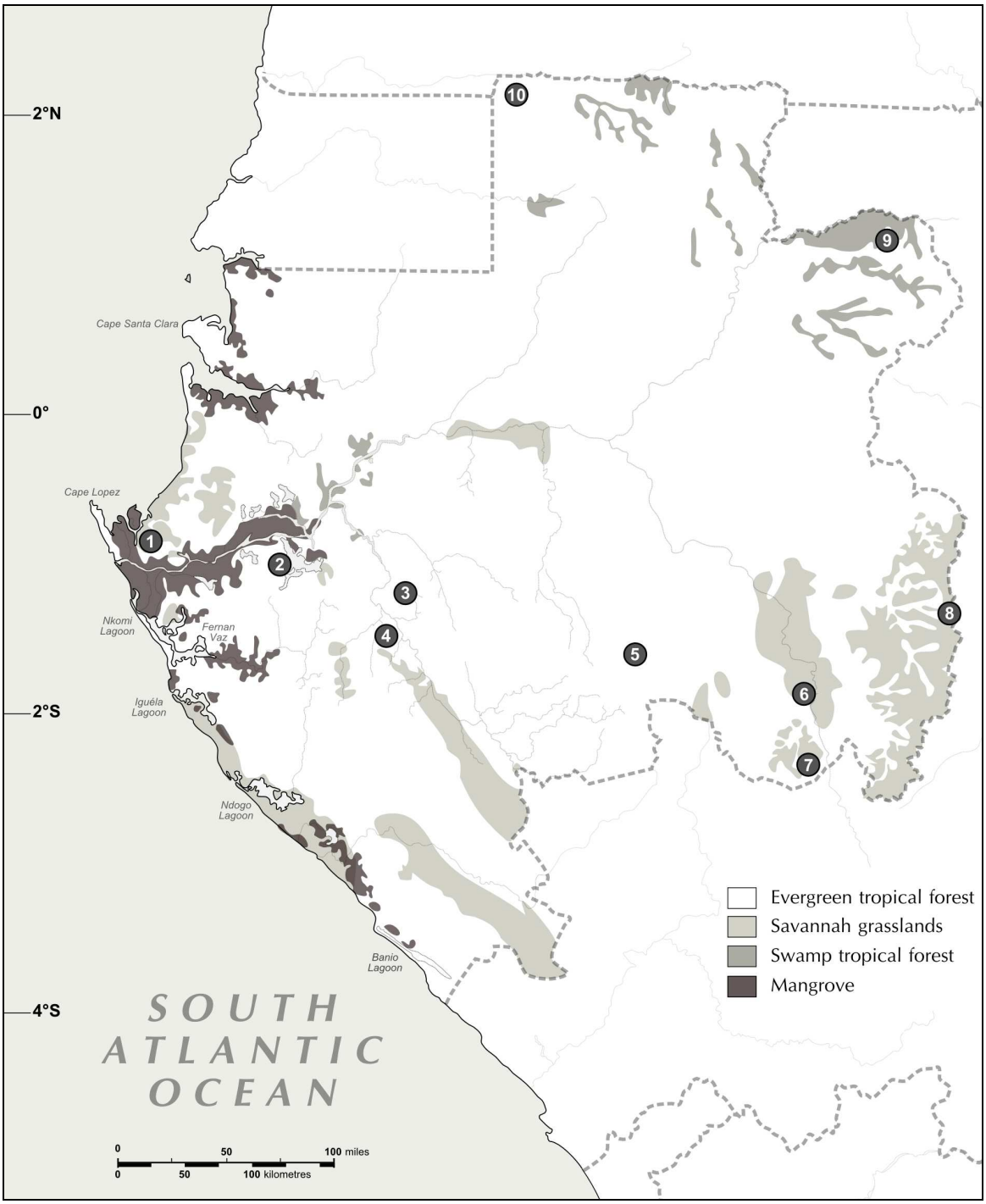

**Map A2. Major population migrations in Gabon**. Most populations seem to have migrated from the North-East (except the Punu and the Lumbu). The Fang were the last migrants. They expanded from northern Gabon in the second half of the 19th century. The Mpongwe (Myènè), on the contrary, were already present on the coast of Gabon in the 14th century. The Tsogho most likely expanded from the upper Ivindo in the 16th century. Little is known about the other groups, and the timeline of their installation in Gabon is mostly speculative. Study sites (❶ to ❿) are reported on the map. Data from Raponda-Walker (1960), Sautter (1966) and Perrois *et al.* (1983).

# A3. Population of Gabon




**Map A3. Population density in Gabon**. About 73% of the population of Gabon (1,500,000 inhabitants) is concentrated in urban areas (Libreville, Port-Gentil, Franceville, Lambaréné). Gabon is under-populated. Average population density is only 5.3 inhabitants x $m^{-2}$, with high variations between regions, and large depopulated areas. Study sites (❶ to ❿) are reported on the map. Data from GRID (2000).

# A4. Vegetation of Gabon




**Map A4. Major agroecological zones in Gabon**. Vegetation in Gabon is rather uniform. Forest covers about 85% of the territory, while savannah grasslands represent only 15%. Forest areas also include mangroves around the lagoons (Nkomi, Iguéla, Banio) and the Gabon estuary. Study sites (❶ to ❿) are reported on the map. Data from Caballé & Fontès (1977).

# Supplementary material

# B1. Typology of farmers

**Table B1. Typology of farmers** interviewed in in a) Odimba, b) Nombedouma, c) Douani, d) Mandilou, e) Makoula, f) Mopia, g) Mouyabi, h) Odjouma, i) Imbong, j) Mbong-Ete. The large majority of my informants (192/201) were women (♂ indicates where the interviewee was a man). Ages indicated are an approximation.

### a. Odimba

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| RN | 40 | Port-Gentil | Orungu (B.11b) | *Avori* | *Aziza* |
| AH | 50 | Port-Gentil | Orungu (B.11b) | *Anouva* | *Ananga* |
| NF | 60 | Nkendje | Orungu (B.11b) | *Agendje* | *Agondjo* |
| ZJ | 65 | Omboué | Nkomi-Orungu | *(Nkomi)* | *(Orungu)* |
| MM♂ | 55 | Ossewé | Punu (B.43) | *Boudjala* | *Boudjala* |
| IF♂ | 40 | Moabi | Punu (B.43) | *Boudjala* | *Ibassa* |
| MF♂ | 40 | Mayumba | Vili (H.12) | *Bivabiluango* | *Baghambo* |
| AC | 70 | Oloumi | Akele (B.22) | *Boudieyi* | *Bubuka* |
| MD | 55 | Azingo | Vili-Nkomi (B.11e) | *(Vili)* | *(Nkomi)* |
| MC | 50 | Sette-Cama | Punu (B.43) | *Iongo* | *Boudjala* |
| BB | 40 | Moabi | Punu (B.43) | *Boudjala* | *Boudjala* |
| MT | 50 | Sette-Cama | Punu (B.43) | *Iongo* | *Boudjala* |

### b. Nombedouma

| Farmers | Age | Village of birth | Ethnic group | Father lineage* | Mother lineage |
|---|---|---|---|---|---|
| OMF | 60-65 | Ompomouena | Galwa (B.11c) | — | *Adjavi* |
| NJ | 50 | Nombedouma | Galwa (B.11c) | — | *Akaza* |
| OM | 50 | Nombedouma | Galwa (B.11c) | — | *Avandji* |
| IMT | 45 | Nengue-Ntogolo | Galwa (B.11c) | — | *Avandji* |
| OC♂ | 52 | Port-Gentil | Galwa (B.11c) | — | *Avandji* |
| $AG_1$ | 40-45 | Nombedouma | Galwa (B.11c) | — | *Avandji* |
| IL | 55-60 | Nombedouma | Galwa (B.11c) | — | *Awuru* |
| NM | 30 | Nombedouma | Galwa (B.11c) | — | *Avandji* |
| AA | 65-70 | Bumba | Galwa (B.11c) | — | *Avandji* |
| NF | 60-65 | Nombedouma | Galwa (B.11c) | — | *Awuru* |
| OJ | 60 | Nombedouma | Galwa (B.11c) | — | *Akaza* |
| $AG_2$ | 60-65 | Nombedouma | Galwa (B.11c) | — | *Avandji* |
| OF | 30 | Nombedouma | Galwa (B.11c) | — | *Awuru* |
| IG | 30 | Nombedouma | Galwa (B.11c) | — | *Awuru* |

*****The Myènè are a matrilineal society. Only the mother lineage was recorded in Nombedouma.

**c. Douani**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| MAF | 30 | Fougamou | Ghisir (B.41) | *Simbu* | *Bouloulou* |
| NJ | 30 | Mimongo | Tsogho (B.31) | *Gheongo* | *Motoka* |
| BBH | 60 | Fougamou | Eviya (B.301) | *Bupeti* | *Ifuba* |
| LMF | 60 | Fougamou | Ghisir (B.41) | *(Balumbu)* | *Bululu* |
| KA | 30 | Ikobe | Tsogho (B.31) | *Iongo* | *Osembe* |
| MC | 45-50 | Douani | Tsogho (B.31) | *Gassanga* | *Osembe* |
| DV | 45 | Matadi | Eviya (B.301) | *(Tsogho)* | *Motoka* |
| BI | 25 | Oyenano | Tsogho (B.31) | *Rambe* | *Motoka* |
| DL | 30 | Fougamou | Tsogho (B.31) | *Gassanga* | *Motoka* |
| PJ | 50 | Matadi | Tsogho (B.31) | *Pogio* | *Motoka* |
| KA | 60 | Matende | Tsogho (B.31) | *Motoka* | *Ndjobe* |
| MV | 55 | Moghoko | Tsogho (B.31) | *Motoka* | *Ndjobe* |
| BL | 60 | Biogho | Tsogho (B.31) | *Pogio* | *Gheongo* |
| KMF | 25-30 | Sindara | Tsogho (B.31) | *Gheongo* | *Ndjobe* |
| OC | 40-45 | Douani | Tsogho (B.31) | *Gassanga* | *Osembe* |

**d. Mandilou**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| MR | 50-55 | Yombi | Ghisir (B.41) | *Bouyala* | *Boumango* |
| MZ♂ | 50-55 | Mouponou | Ghisir (B.41) | *Ghirendi* | *Bubuka* |
| $MA_1$ | 60-65 | Dubanga | Ghisir (B.41) | *Bundiga* | *Bupiti* |
| $MMJ_1$ | | St-Pierre | Ghisir (B.41) | *Mombi* | *Ghirendi* |
| $MA_2$ | 30-40 | Fougamou | Ghisir (B.41) | *Minanga* | *Ghirendi* |
| $MA_3$ | 65 | Bougounga | Ghisir (B.41) | *Buyombu* | *Bundinga* |
| DH | 55-60 | Tsangudimbu | Ghisir (B.41) | *Bupeti* | *Mombi* |
| $MMJ_2$ | 60 | Moabi | Punu (B.42) | *Badumbi* | *Ghimondu* |
| NH | | Guidouma | Ghisir (B.41) | *Monbi* | *Mupeti* |
| $KB_1$ | 60 | Yombi | Ghisir (B.41) | *Bupeti* | *Bubuka* |
| $BA_1$ | 60 | Guignonga | Ghisir (B.41) | *Bupeti* | *Bupeti Malunga* |
| NM | 50 | Guidouma | Ghisir (B.41) | *Bumambu* | *Ghibassa* |
| MT | 55-60 | Mouponou | Ghisir (B.41) | *Minanga* | *Bubuka* |
| NJ | 60 | Tsangudimbu | Ghisir (B.41) | *Bupeti* | *Mombi* |
| GM | 55-60 | Mouila | Ghisir (B.41) | *Bundiga* | *Bupeti* |
| MM | 65-70 | Mitsangi | Ghisir (B.41) | *Boudieyi* | *Mombi* |
| PMA | 65 | Tsangudimbu | Ghisir (B.41) | *Boumboungo* | *Bupeti* |
| DMG | 45-50 | Mandilou | Ghisir (B.41) | *Mombi* | *Budieghi* |
| DB | 25-30 | Mandilou | Ghisir (B.41) | *Bubuka* | *Budieghi* |
| $KB_2$ | 30-35 | Fougamou | Ghisir (B.41) | *Minongu* | *Buyombu* |
| TF | 25-30 | Booué | Ghisir (B.41) | *Boumboungo* | *Buyombu* |
| $BA_2$ | 50-55 | Zanakeri | Ghisir (B.41) | *Bundinga* | *Bupeti* |
| BG | | Ngabu | Ghisir (B.41) | *Bupeti* | *Buyombu* |
| SH | 55 | Pagadianzi | Ghisir (B.41) | *Bundinga* | *Bupeti* |
| BJC♂ | 45-50 | Mukiba | Ghisir (B.41) | *Ghimondo* | *Bupeti* |
| DC | 65-70 | Guidouma | Ghisir (B.41) | *Ghimondo* | *Ghibassa* |
| BR | 50-55 | Mouila | Ghisir (B.41) | *Bumombu* | *Ghibassa* |
| NF | 50-55 | Lambaréné | Ghisir (B.41) | *Budieghi* | *Mitsimba* |

**e. Makoula**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| TJ | 40 | Makoula | Ndzabi (B.52) | *Mwanda* | *Baghouli* |
| NC | 25-30 | Mamongo | Ndzabi (B.52) | *Iongo* | *Maghamba* |
| MMF | 55 | Makoula | Ndzabi (B.52) | *Basomba* | *Nianga* |
| $MA_1$ | 55 | Mbigou | Ndzabi (B.52) | *Maghambu* | *Baguli* |
| NV | 25-30 | Boundzi | Ndzabi (B.52) | | |
| PC | 70 | Mayela | Bongo (Pygmy) | *Bajangu* | *Basomba* |
| BC | 30 | Makoula | Ndzabi (B.52) | *Bapungu* | *Maghambu* |
| MT | 50 | Mouyaya | Ndzabi (B.52) | *Yeyi* | *Mitchimba* |
| NA | 60 | Ndzugu | Ndzabi (B.52) | *Niangu* | *Yeyi* |
| NS | 25-30 | Ndubi | Bongo (Pygmy) | *Basomba* | *Maghambu* |
| BS | 65-70 | Moussandi | Bongo (Pygmy) | *Bouyola* | *Maghambu* |
| $MA_2$ | 50 | Makoula | Bongo (Pygmy) | *Papungu* | *Maghambu* |
| NF | 35-40 | Moussanda | Bongo (Pygmy) | *Maghumbu* | *Ghiongo* |
| MH | 65-70 | Possi | Bongo (Pygmy) | *Maghambo* | *Basomba* |
| BE | 25-30 | Bakumba | Ndzabi (B.52) | *(Fang)* | *Chongo* |
| $MA_3$ | 50-55 | Moussanda | Bongo (Pygmy) | *Bouvala* | *Maghambo* |

**f. Mopia**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| GM | 40-45 | Mopia | Tsaayi (B.73a) | | |
| NB | 30 | Mopia | Kaningi (B.602) | *Moussangui* | *Likuala* |
| BM | 60-65 | Dumay | Kaningi (B.602) | *Moutsay* | *Moutsay* |
| MS | 35-40 | Mopia | Kaningi (B.602) | *Sawanza* | *Saluku* |
| KV | 60-65 | Bandoy (Congo) | Tsaayi (B.73a) | | |
| BH | 60 | Sibi | Ndasa (B.28) | | |
| MG | 30-35 | Franceville | Kaningi (B.602) | *Moubolo* | *Moupia* |
| MV | 60 | Punga | Kaningi (B.602) | *Buma* | *Kimi* |
| BB | 35-40 | Otou | Teke (B.71) | | |
| $NE_1$ | 35-40 | Franceville | Kaningi (B.602) | | |
| KH | 35-40 | Komono (Congo) | Wumbu (B.78) | | |
| MC | 35-40 | Mopia | Kaningi (B.602) | | |
| OY | 45-50 | Mopia | Mbanwe (B.23) | | |
| KA | 55-60 | Mopia | Kaningi (B.602) | *Motati* | *Mokanini* |
| TP | | Ganda | Kota (B.25) | | |
| $NE_2$ | 40-45 | Mopia | Mbamba (B.62) | | |
| KMM | 30-35 | Mopia | Kaningi (B.602) | *Mania* | *Ndjomuete* |
| NYM | 60 | Mopia | Wumbu (B.78) | | |
| KC | 50-55 | Mango | Kaningi (B.602) | *Mbuma* | *Motati* |
| OC | 25-30 | Lovenza (Congo) | Ndasa (B.28) | | |
| MP | 25-30 | Zamaga (Congo) | Wumbu (B.78) | | |

**g. Mouyabi**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| $MH_1$ | 50 | Mouyabi | Bongo (Pygmy) | *Makana* | *Kiongo* |
| $MH_2$ | 30 | Mouyabi | Bongo (Pygmy) | *Nguono* | *Kiongo* |
| NC | 40 | Mouyabi | Bongo (Pygmy) | *Makana* | *Makana* |
| $MA_1$ | 30 | Mouyabi | Bongo (Pygmy) | *Kiongo* | *Ndzuama* |
| MY | 25-30 | Mouyabi | Bongo (Pygmy) | *Makana* | *Kiongo* |
| MP | 25-30 | Mouyabi | Bongo (Pygmy) | *Makana* | *Kiongo* |
| MT | 55--60 | Mouyabi | Bongo (Pygmy) | *Makana* | *Enamini* |
| KM | 60-65 | Mouyabi | Bongo (Pygmy) | *Motati* | *Kiongo* |
| $MA_2$ | | Mouyabi | Bongo (Pygmy) | | |
| BH | | Mouyabi | Bongo (Pygmy) | *Motati* | *Bouyala* |
| LN | 25-30 | Mouyabi | Bongo (Pygmy) | *Ibià* | *Kiongo* |
| KJ | 25-30 | Mouyabi | Bongo (Pygmy) | *Bouyala* | *Makana* |
| MM | 20-25 | Mouyabi | Bongo (Pygmy) | *Kiongo* | *Mouyala* |
| MN | 20-25 | Mouyabi | Bongo (Pygmy) | *Makana* | *Mbuma* |
| MF | 25-30 | Mouyabi | Bongo (Pygmy) | *Djuama* | *Mbum* |

**h. Odjouma**

| Farmers | Age | Village of birth | Ethnic group | Father lineage | Mother lineage |
|---|---|---|---|---|---|
| AG | | Djogo | Teke (B.71) | *Ebili* | *Otali* |
| TA | | Djogo | Teke (B.71) | *Buma* | *Luri* |
| FP | | Djogo | Teke (B.71) | *Okama* | *Nkomo* |
| MC | | Ossoele | Teke (B.71) | *Akaga* | *Kala* |
| KM | | Akabi | Teke (B.71) | *Mpumu* | *Okama* |
| $EP_1$ | | Labiri (Congo) | Teke (B.71) | *Luri* | *Mpumu* |
| AM | | Djogo | Teke (B.71) | *Nkomo* | *Ntsa* |
| BD | | Labiri (Congo) | Teke (B.71) | *Ekaga* | *Nkomo* |
| MV | | Lekori | Teke (B.71) | *Olua* | *Mboma* |
| OC | | Oyouo | Teke (B.71) | *Ndjia* | *Ntcha* |
| $OG_1$ | | Djogo | Teke (B.71) | *Moyaya* | *Mbuli* |
| $EP_2$ | | Ia | Teke (B.71) | *Mbuli* | *Olua* |
| EC | | Ongali | Teke (B.71) | *Oluna* | *Olua* |
| AA | | Oyouo | Teke (B.71) | *Mondjumu* | *Ebili* |
| OB | | Lekuna (Congo) | Teke (B.71) | *Obagi* | *Osama* |
| EA | | Lemvele (Congo) | Teke (B.71) | *Kasuele* | *Modjaga* |
| EJ | | Oyouo | Teke (B.71) | *Djuani* | *Osama* |
| $OJ_1$ | | Djogo | Teke (B.71) | *Ntchumu* | *Lakila* |
| $AJ_1$ | | Untcho | Teke (B.71) | *Djubuga* | *Okama* |
| OV | | Djogo | Teke (B.71) | *Makatulu* | *Ewa* |
| $OJ_2$ | | Lekori | Teke (B.71) | *Modjua* | *Ntcha* |
| TV | | Djogo | Teke (B.71) | *Olua* | *Mboma* |
| PH | | Taba (Congo) | Teke (B.71) | *Modjaga* | *Mboma* |
| AH | | Ongali | Teke (B.71) | *Ndjia* | *Otari* |
| $OG_2$ | | Djogo | Teke (B.71) | *Mandiagi* | *Mpumu* |
| $AJ_2$ | | Bibaya (Congo) | Teke (B.71) | *Mpumu* | *Iagi* |
| IM | | Lekori | Teke (B.71) | *Olua* | *Akieni* |
| LA | | Djogo | Teke (B.71) | *Mimbu* | *Kumu* |
| KS♂ | | Djogo | Teke (B.71) | *Mpumu* | *Makasini* |
| AP | | Djogo | Teke (B.71) | *Ekala* | *Lakila* |
| BM | | Djogo | Teke (B.71) | *Mpumu* | *Okama* |

Based on data collected in 2004 (see Delêtre 2004).

**i. Imbong**

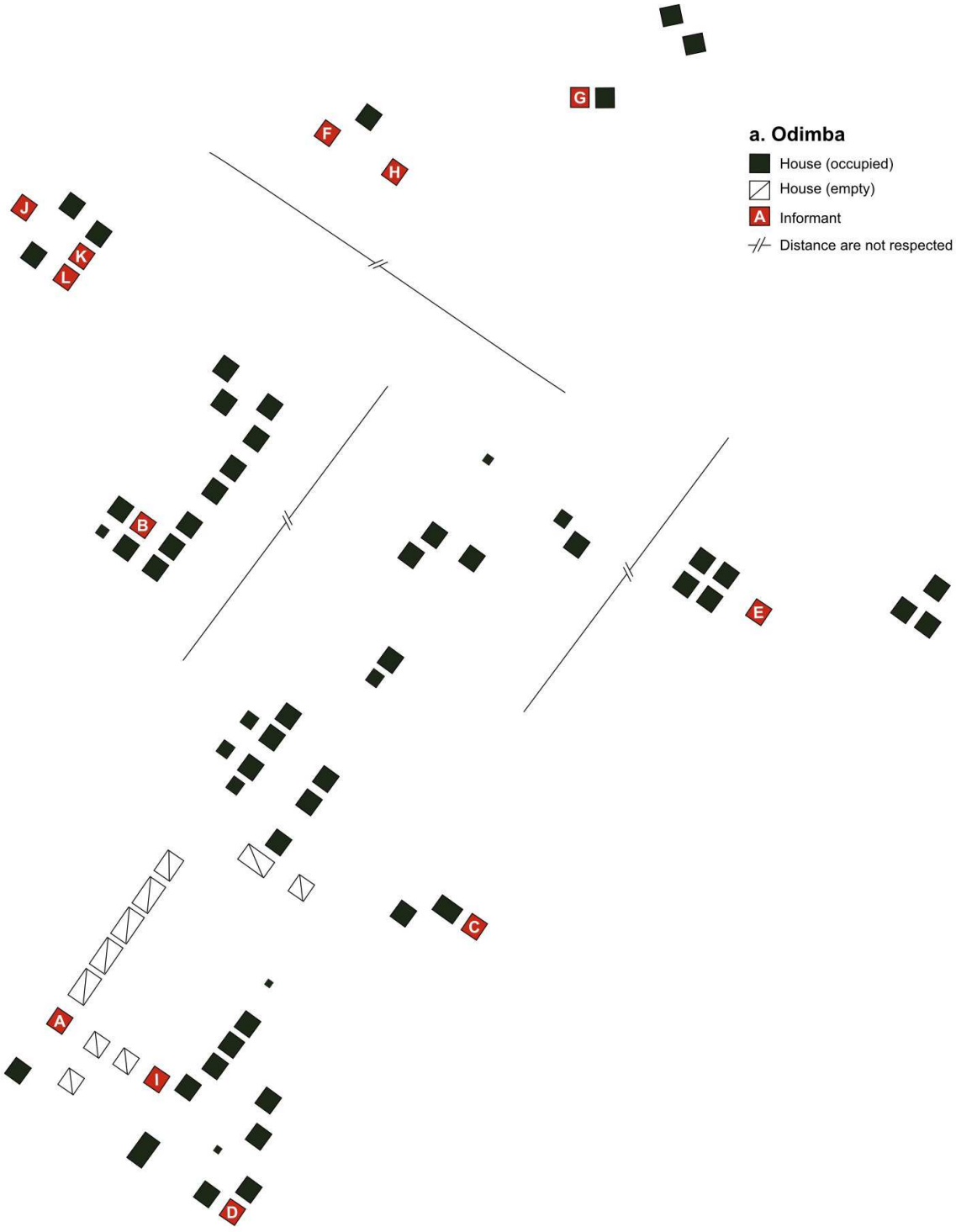
| Farmers | Age | Village of birth | Ethnic group | Father lineage |
|---|---|---|---|---|
| MG | 40-45 | Imbong | Kwele (A.85b) | |
| $MC_1$ | 35-40 | Zula | Koya (Pygmy) | *Samuadi* |
| $MC_2$ | 25-30 | Imbong | Koya (Pygmy) | *Samoaz* |
| $ME_1$ | 35-40 | Imbong | Koya (Pygmy) | *Masaka* |
| NH | 45-50 | Ibea | Koya (Pygmy) | *Sakunda* |
| NA | 50-55 | Imbong | Kwele (A.85b) | *Ibo'o* |
| EC | 50-55 | Imbong | Kwele (A.85b) | *Sakienda* |
| NS | 30-35 | Zula | Koya (Pygmy) | *Sangwagna* |
| BR♂ | 35-40 | Imbong | Mwessa (B.20) | *Sassolo* |
| IG | 25-30 | Itangae | Koya (Pygmy) | *Sakunda* |
| ZN | 30-35 | Imbong | Koya (Pygmy) | *Oyemba* |
| IF | 30 | Zula | Koya (Pygmy) | *Sahussu* |
| MO | 50-55 | Imbong | Mwessa (B.20) | *Sabe* |
| ZP | 55-60 | Mawa | Koya (Pygmy) | *Oyemba* |
| $ME_2$ | 30 | Imbong | Koya (Pygmy) | *Sabo* |
| IC | 30-35 | Imbong | Koya (Pygmy) | |
| ZR | 45-50 | Imbong | Kwele (A.85b) | *Sasanza* |
| IA | 55-60 | Imbong | Koya (Pygmy) | *Oyemba* |
| MD | 25-30 | Imbong | Koya (Pygmy) | *Samuadi* |
| MN | 25-30 | Imbong | Koya (Pygmy) | *Sabo* |
| MS | 40 | Imbong | Koya (Pygmy) | *Sabo* |

**j. Mbong-Ete**

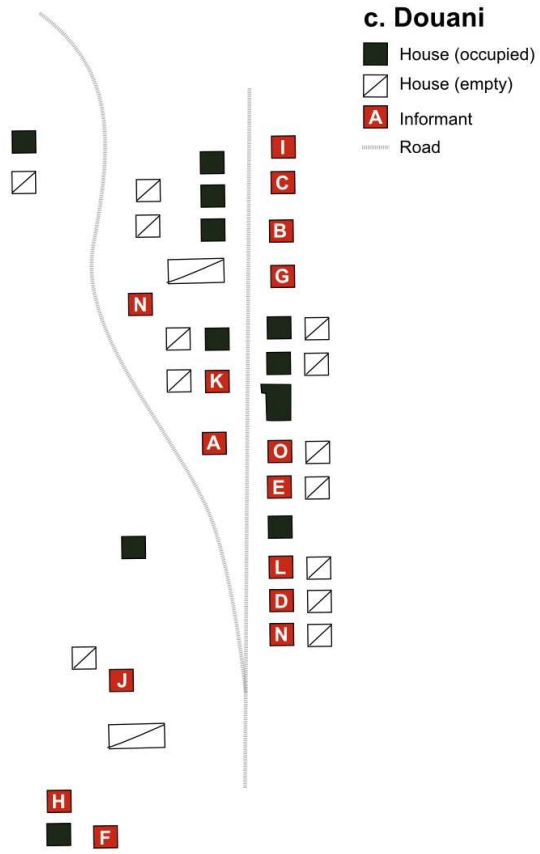
| Farmers | Age | Village of birth | Ethnic group | Father lineage |
|---|---|---|---|---|
| NAM | 45 | Edoum (Cameroon) | Ntumu (A.75a) | *Esambe* |
| NZG | 45-50 | Agnizok | Ntumu (A.75a) | *Essandon* |
| $NEI_1$ | 60-65 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| EM | | Ovang | Ntumu (A.75a) | *Essandon* |
| NMC | 30-35 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| EC | 30 | Minang (Equatorial Guinea) | Ntumu (A.75a) | *Essandon* |
| MH | 30-35 | Nkol-Ekon (Cameroon) | Ntumu (A.75a) | *Eba* |
| MMJ | 30 | Zaminkan (Cameroon) | Ntumu (A.75a) | *Essabe* |
| AAL | 55-60 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| BZS | 60-65 | Fen | Ntumu (A.75a) | *Nkodje* |
| NOL | 50-55 | Ngon (Equatorial Guinea) | Ntumu (A.75a) | *Esseng* |
| NMM | 30 | Nkoum-Ekeke (Cameroon) | Ntumu (A.75a) | *Gakein* |
| OL | | Nkoum-Ekeke (Cameroon) | Ntumu (A.75a) | *Gakein* |
| AOB | 30-40 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| OOI | 20 | Mokomo (Cameroon) | Ntumu (A.75a) | *Essakounane* |
| AE | 35-40 | Afan-Gui (Equatorial Guinea) | Ntumu (A.75a) | *Essahong* |
| BP | 50 | Adzap-Essatop | Ntumu (A.75a) | *Essatop* |
| NOG | 55-60 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| EOJ | 50-55 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| AJ | 40-45 | Zaminkan (Cameroon) | Ntumu (A.75a) | *Essabe* |
| NMJF♂ | 35-40 | Mbong-Ete | Ntumu (A.75a) | *Effak* |
| AMT | 60-65 | Fen | Ntumu (A.75a) | *Nkodje* |
| ONJ | | Nkoum-Ekeke (Cameroon) | Ntumu (A.75a) | *Gakein* |
| ZAM | 65 | Bikougou | Ntumu (A.75a) | *Eba* |
| OZJ | | Agnizok | Ntumu (A.75a) | *Essandon* |
| AEV | 45-50 | Nkol-Mengoua | Ntumu (A.75a) | *Essabe* |
| $NEI_2$ | 65 | Ozakoung | Ntumu (A.75a) | *Essabeng* |
| MET | 60 | Misele | Ntumu (A.75a) | *Essandon* |

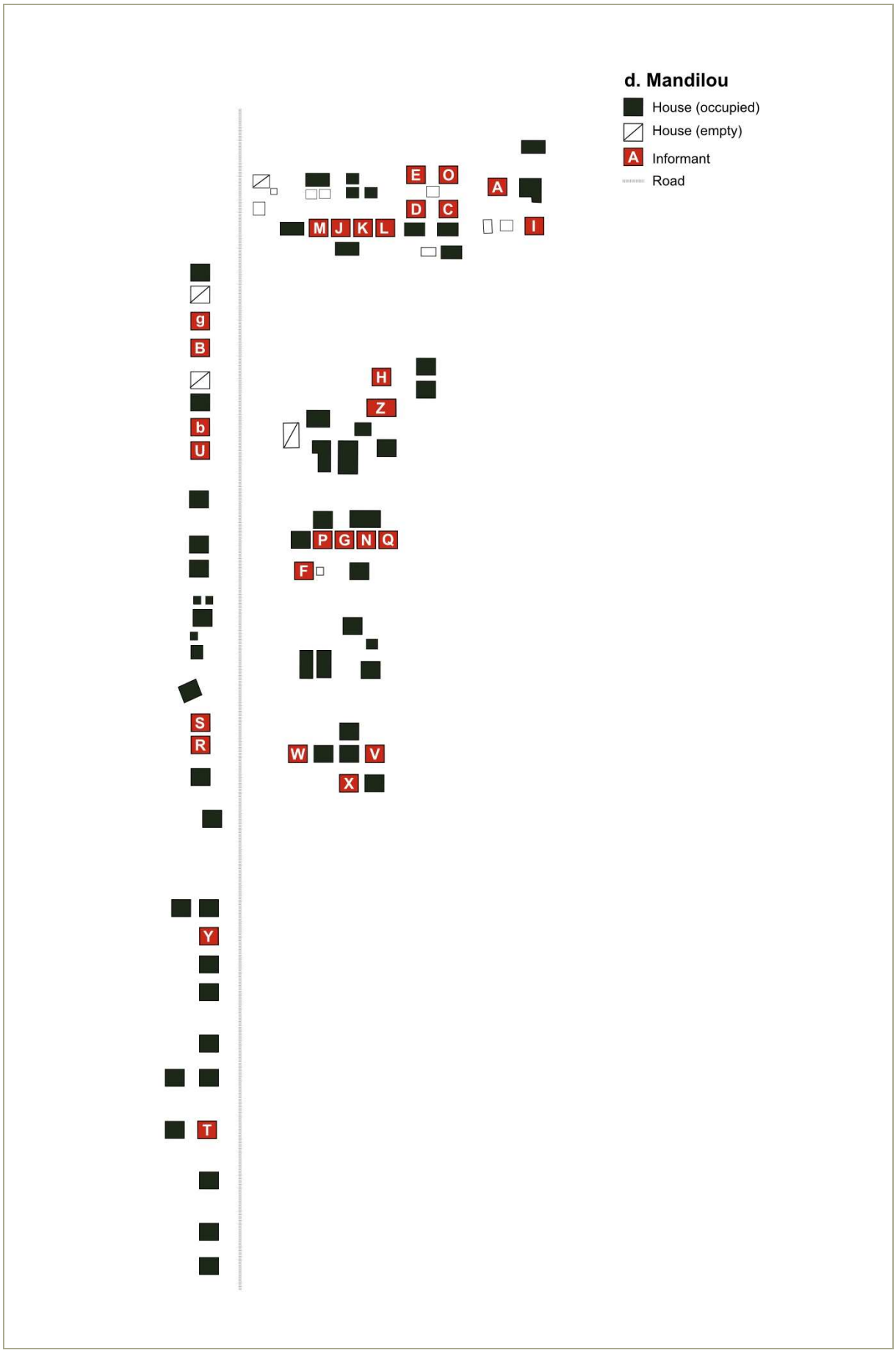
# B2. Village maps

**Figure B4. Map of the villages studied** showing the distribution of informants in a) Odimba, b) Nombedouma, c) Douani, d) Mandilou and e) Mbong-Ete. Maps were drawn to ensure that the sample covered the whole community, but also avoided biases associated with the frequent organization of villages into districts of relatives. All maps are oriented with the North at the top.




b. Nombedouma
House (occupied)
House (empty)
A Informant
Coast
S
M
E
N1
N2
H
I
B
B
C
C
K
A
F
G
L
D
D


c. Douani
House (occupied)
House (empty)
A Informant
Road
I
C
B
G
N
K
A
O
E
L
D
N
J
H
F


d. Mandilou
House (occupied)
House (empty)
Informant
Road
E
O
A
D
C
M
J
K
L
I
g
B
H
Z
b
U
P
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Q
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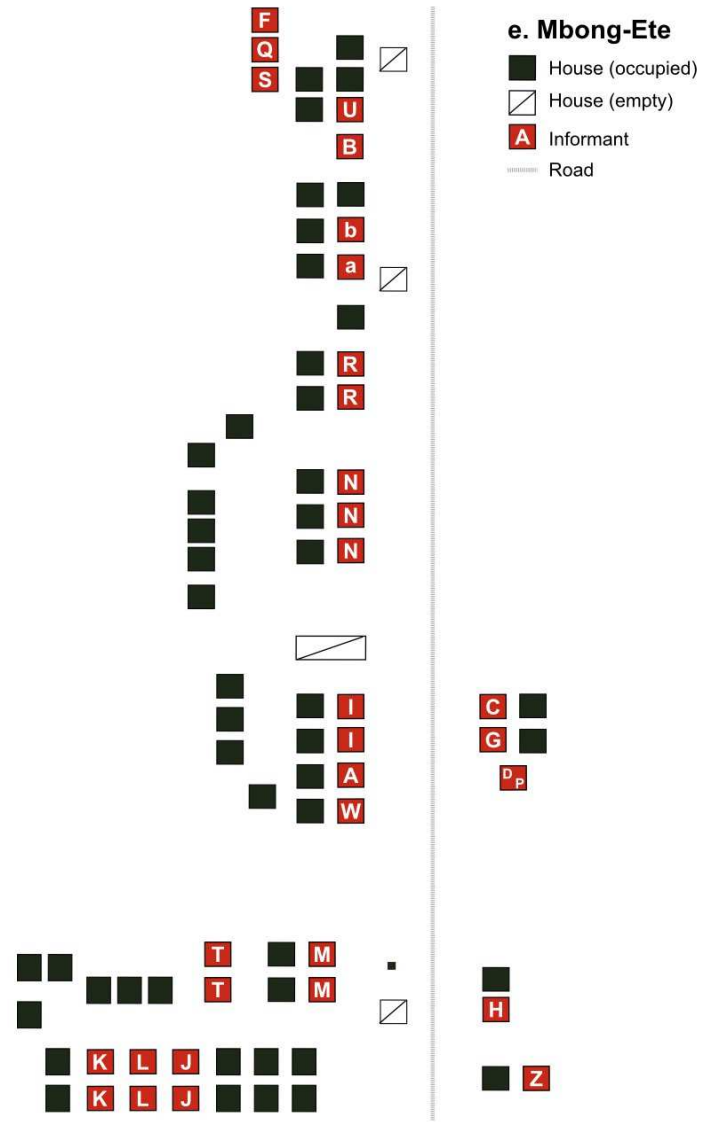
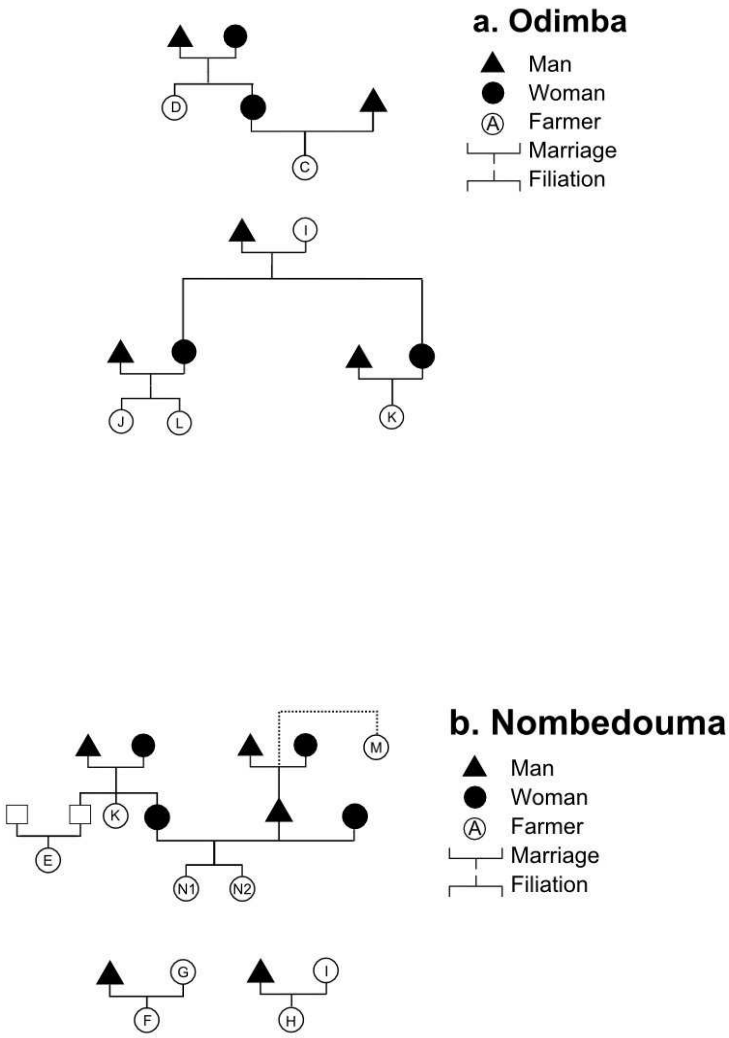
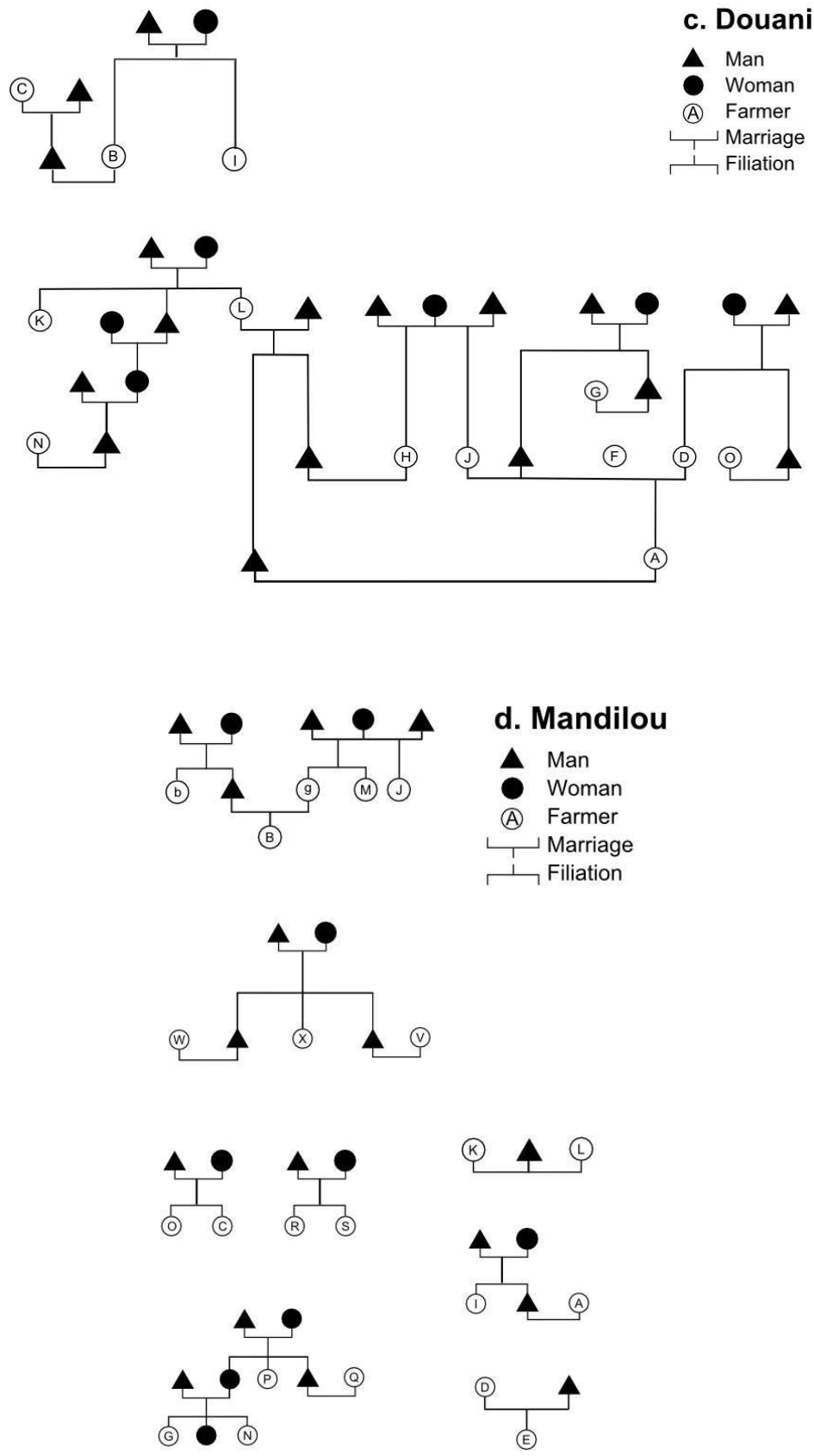
W
V
X
Y
T

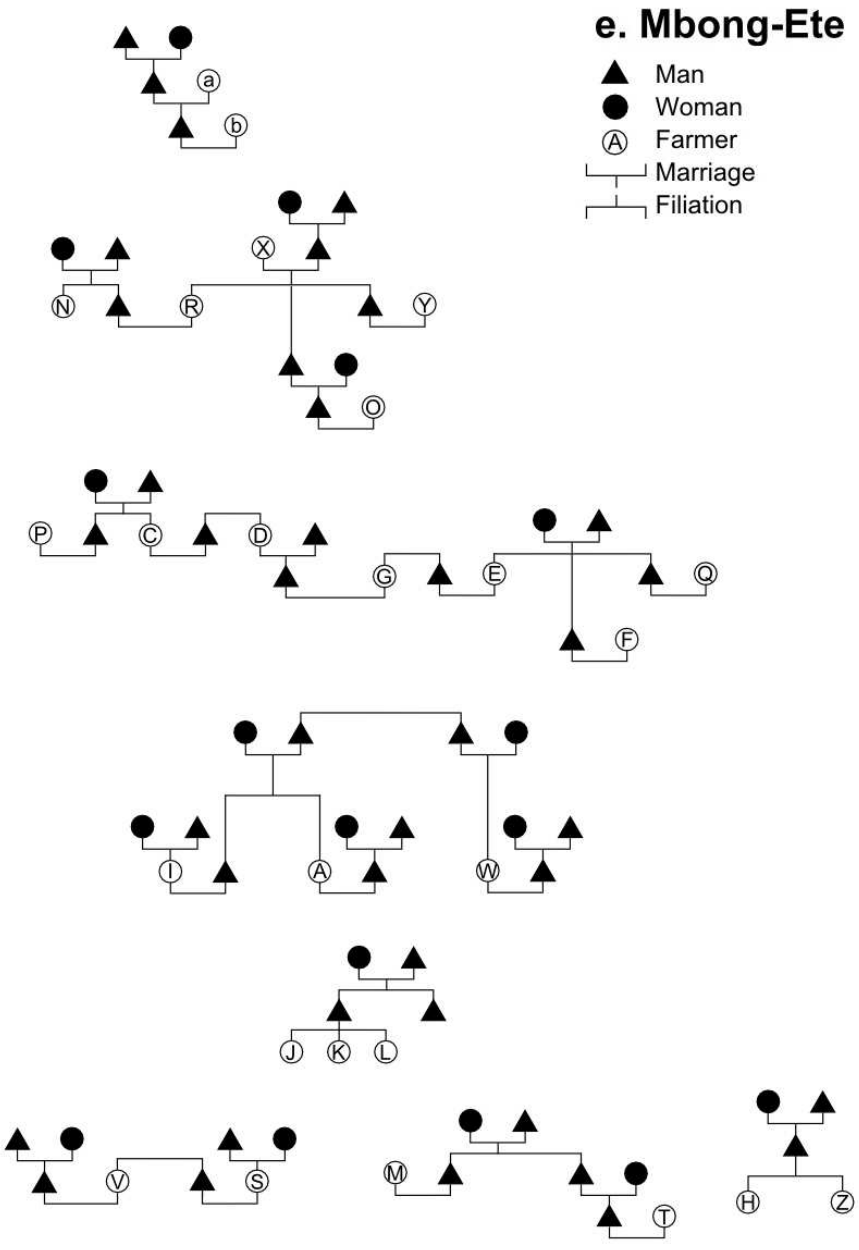

e. Mbong-Ete
House (occupied)
House (empty)
Informant
Road
F
Q
S
U
B
b
a
R
R
N
N
N
I
I
A
W
C
G
D
P
T
T
M
M
H
K
L
J
K
L
J
Z

# B3. Farmers' kinship relationships

**Figure B3. Kinship networks** for the sub-sample of farmers interviewed in a) Odimba (no information was available for farmers A, B, E, F, G, H, L), b) Nombedouma (no information was available for farmers A, B, C, D, E, J, L), c) Douani (no information was available for farmers E and M), d) Mandilou (no information was available for farmers F, H, T, U, Y, Z, a), e) Mbong-Ete (no information was available for farmers B and U).




c. Douani
Man
Woman
Farmer
Marriage
Filiation
C
B
I
K
L
N
H
J
G
F
D
O
A
d. Mandilou
Man
Woman
Farmer
Marriage
Filiation
b
g
M
J
B
W
X
V
O
C
R
S
K
L
I
A
P
Q
G
N
D
E


e. Mbong-Ete
Man
Woman
Farmer
Marriage
Filiation
a
b
X
N
R
Y
O
P
C
D
G
E
Q
F
I
A
W
J
K
L
V
S
M
T
H
Z

# B4. Inventory of landraces

**Table B4. Inventory of the 355 emically identified landraces in Gabon** (in total, 406 names), with mention of their origin, geographical distribution, etymology, and known alternative names (=). Additional data collected from the literature were included. Corresponding languages are referred to by a code, following Guthrie's classification of Bantu languages (Guthrie 1948) revised by Maho (2003). Not all synonymies have been formally established. (?) indicates where the synonymy is likely but could not be confirmed. The list also omits 45 'unknown' landraces (6 recorded in Odimba, 3 in Nombedouma, 26 in Mopia, 5 in Mouyabi, 3 in Imbong and 2 in Odjouma).

[a] Data taken from the literature: Γ Angladette (1949), Δ Raponda-Walker & Sillans (1961), Θ Sautter (1966), ¥ Guillot (1970), Π Adam (1980), Ψ Gaulme (1981), β Rossel (1987), Ω Dounias (1993), δ Binot (1998), £ Van der Veen & Bodinga-bwa-Bodinga (2002), Я Soengas (2010)

● Grown from volunteer seedling

[b] Geographical origin: *Ca* Cameroon, *Co* Congo, *Eq* Equatorial Guinea, *ST* São Tomé

[c] Distribution: *Es* Estuaire, *HO* Haut-Ogooué, *MO* Moyen-Ogooué, *Ng* Ngounié, *Ny* Nyanga, *OI* Ogooué-Ivindo, *OL* Ogooué-Lolo, *OM* Ogooué-Maritime, *WT* Woleu-Ntem

[d] Morphological characteristics: *w* white, *y* yellow, *i* ivory, *p* pink fleshed roots, (2) number of recognized morphotypes.

[e] Remarkable agronomic traits: (*6*, *8*, *12*) short, intermediate, long cycle; *R* resistant to rot, *s* susceptible to rot; *Y* highly productive

[f] Organoleptic properties: *B* bitter, *S* sweet, *I* intermediate

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 1 | *Abaga-mboe* Δ | | A.75 | | Ca? | WT? | | | S |
| 2 | *Aboc-Metoc* Δ | | A.75 | | Ca? | WT? | | | B |
| 3 | *Aboï* Я | | | | | OI | | | S |
| 4 | *Adyanu* ● | | B.11 | | Ga | MO | | | S |
| 5 | *Adzoro* | | A.75 | | Ca | Ca, Eq, WT | w | R | B |
| | | = *Adzora* δ | A.75 | | Ca | OI | | | I |
| | | = *Adzoro-Mbõng* Γ | A.75 | | Ca | Ca, WT | | | B |
| 6 | *Afouba-Mbõng* | | A.75 | (Generic name for sweet manioc) | Ca | Ca, Eq, WT, Es | | | S |
| | | = *Afobo* Γ,Ω, *Afobo-Mbõng* Γ | A.75 | | Ca | Ca, Es | | | S |
| | | = *Akwama-Mbõng* | A.75 | | Ca | WT, Es | | | S |
| | | = *Dame Alice* | | | Ca | WT, Es | | | S |
| | | = *Matati* | A.75 | | Ca | WT | (4) | | S |
| | | = *Bitam, Bitame* Я, *Bitami* Я | | | Ca | OI, Es | | | |
| | | = *Gõndoyem* | | The lady from Oyem | Ca | Ng | w | 6 | S |
| | | = *Ngõngeoyem* δ | | | | OI | | | |
| | | = *Gõndaoyem* Я | | | | OI | | | |
| | | = *Ngoneyem* | | | Ca | Ng, Es | | | S |
| | | = *Côte d'Ivoire* | | | Ca | OM, Es | | | S |
| | | = *Muma, Lemumu, Lemuma* | | | Ca | OL, Es | w | | S |
| 7 | *Afún* | | | | | OI | | | B |
| | | = *Afunu* Я | | | | OI | | | B |
| 8 | *Aima* Я | | | | | OI | | | |
| 9 | *Akora* Δ | | B.21 | | | | | | B |
| 10 | *Akoulwé* Θ | | B.11 | | | MO | | | ? |
| 11 | *Akumikara* | | | | | OI | | | S |
| | | = *Akunekare* | | | | OI | | | S |
| | | = *Kumkare* | | | | OI | | | S |
| | | = *Akunikare* Я | | | | OI | | | S |
| | | = *Akunikarle* Я | | | | OI | | | S |
| | | = *Akunikarla* Я | | | | OI | | | S |
| 12 | *Akunuku* | | | | | OI | | | S |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 13 | *Ãmbaze* | | B.11 | (Island on the lake Onangue) | | MO | | | S |
| 14 | *Ãmbia N'Idjõmba* | | B.11 | Dowry | | OM | | | B |
| 15 | *Amungu* | | B.71 | (Lastname) | | HO | | | ? |
| 16 | *Ãndamebeka* Я | | A.85b? | Walks along in the ceremonies (?) | | OI | | | ? |
| 17 | *Ãnzein* | | | | | OI | | | B |
| | | = *Ãnzeni* Я | | | | OI | | | B |
| | | = *Inzein* Я | | | | OI | | | B |
| | | = *Inzendji* Я | | | | OI | | | B |
| | | = *Dinzeñi* Я | | | | OI | | | B |
| | | = *Lazeñi* Я | | | | OI | | | B |
| 18 | *Asoa* Δ | | B.62 | | | HO | | | B |
| 19 | *Assidieke* | | B.11 | (Lastname) | | OM | | | B |
| 20 | *Assiga* Θ | | A.75 | | Ca? | WT, Es? | | | B |
| 21 | *Assiga-Bwa* Θ | | A.75 | | Ca? | WT, Es? | | | B |
| 22 | *Asuga-Mbõng* Δ | | A.75 | | Ca? | MO | | | B |
| 23 | *Asuku* | | B.71 | Franceville | Ga? | HO | | | B |
| | | = *Masuku* | B.71 | Franceville | Ga? | HO | | | B |
| 24 | *Atolizo Izõmbi* | | B.11 | Feeds the family | | OM | | | S |
| | | = *Atolizo Ozõmbi* | B.11 | | | MO | | | B |
| 25 | *Ayima* | | | | | OI | | | |
| 26 | *Ayumbo* ●,Θ | | B.11 | (Lastname) | Ga | MO | | | B |
| 27 | *Azame-Mbõng* Δ | | A.75 | | Ca? | WT, Es? | | | S |
| 28 | *Bakãnga* | | | | | Ng | | | B |
| 29 | *Bakõngo*[1] Θ | | B.11 | | Co | OM, MO, Ng, OI? | (2) | 12 | B |
| | | = *Congo, Kõngo* £ | B.301 | | | Ng | | | |
| | | = *Makõngou* δ (?) | | | | OI | | | |
| 30 | *Bakungu* | | | | | Ng | | | B |
| 31 | *Bana* | = *Banié, Bane* Я | | | | OI | | | S |
| 32 | *Baniugui* | | | Bee | | HO | | | B |

[1] Introduced from Brazzaville to Gabon in the 1920s by the grand-daughter of King Denis (Raponda-Walker & Sillans 1961).

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 33 | *Barokisi* | | B.71 | | | HO | | | B |
| 34 | *Bata* | = *Bate Bakõngo* | | | | Ng | w | | B |
| | | = *Ebata* δ | | | | OI | | | |
| | | = *Dinbata* Я, *Mimbata* Я | | | | OI | | | B |
| 35 | *Bèdèbèkalè* Δ | | B.21 | | | | | | S |
| 36 | *Belfutu* | | B.11 | *Artocarpus altilis* (Parkinson), Fosberg, Moraceae | | OM, Ng | w | 12 | S |
| 37 | *Bendoubi* Θ | | A.75 | | | MO | | | ? |
| 38 | *Benge* | | B.52? | Red | | OL | i | | B |
| 39 | *Bête-Bête* | | | | | Ng | | | S |
| 40 | *Boko* | | B.71 | *Rumex acetosa* L., Polygonaceae | | HO | | | B |
| 41 | *Bokoapoto* | | | | | OI | | | |
| 42 | *Bokungu Boduli* | | | | | Ng | | | B |
| 43 | *Bõmbe* Θ | | B.11 | | | MO | | | ? |
| 44 | *Bomvomo* Θ | | A.75 | | | MO | | | ? |
| 45 | *Bõndame Tchinãnga* | = *Bonametinangue* | | Wait for me here | | OI | | | S |
| | | = *Bõndametina* Я | A.85b | | | OI | | | S |
| | | = *Bõndatete* Я (?) | | | | OI | | | S |
| 46 | *Bõndjolãmba* ● | | B.11 | (Village in Gabon) | Ga | OM | | | S |
| 47 | *Bongo* | | | (Lastname) | | HO | | | B |
| 48 | *Boto* Я | | | | | OI | | | S |
| 49 | *Busunasõmbe* | | | | | HO | | | B |
| 50 | *Bwãnga* | | B.11 | (Lastname) | | OM | | | B |
| 51 | *Bwata* | | | | | OL | | | S |
| | | = *Obwata* δ | | | | OI | | | |
| 52 | *Camarun* | | | Cameroon | Ca | OI | | | |
| 53 | *Cécile* ● | | B.11 | (Firstname) | Ga | MO | | | B |
| 54 | *Chua* | | | Stop (?) | | HO | | | B |
| 55 | *Ciam* | | | CIAM[2] | | Es, Ng | | | S |
| 56 | *Cinq Minutes* Ω | | | Cooked in five minutes | | Ca, HO | | | S |
| 57 | *Colette* ● | | B.11 | (Firstname) | Ga | MO | | | B |

[2] Centre d'Introduction et de Multiplication du Matériel Végétal.

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 58 | *Dame Jaune* | | | | | Es, OM, MO, Ng, Ny, OI, OL, HO | y | | S |
| | | = *Madame Jaune* δ, Я | | | | WT, OI | y | | |
| | | = *Brazzaville* | | (City) | | OM, Ng | y | | S |
| | | = *Mokoyo* | | | | HO | y | | B |
| | | = *Dikidikoko* | | Chicken's egg manioc | | Ng | y | | S |
| 58 | *Dame Jaune* | | | Yellow lady manioc | | Es, OM, MO, Ng, Ny, OI, OL, HO | y | | S |
| | | = *Madame Jaune* δ, Я | | | | WT, OI | y | | |
| | | = *Brazzaville* | | (City) | | OM, Ng | y | | S |
| | | = *Mokoyo* | | | | HO | y | | B |
| | | = *Dikidikoko* | | Chicken's egg manioc | | Ng | y | | S |
| | | = *Dikilikoko Di Jaune* | | | | Ng | (2) | | S |
| | | = *Dikilikoko Di Chinois* | | | | | | | |
| | | = *Le Chinois* | | | | | | | |
| | | = *Iake a Tchosso* | | | | | | | |
| | | = *Eake A Tchozo* | | | | | | | |
| | | = *Yakotojo* (?) | | | | | | | |
| | | = *Jaune* | | Yellow manioc | | OM, Ng, HO | y | 12 | S |
| | | = *Ipãndo Jaune* | | | | | | | |
| | | = *Muguwi* | | | | | | | |
| | | = *Make Ta Koko* | B.43 | Chicken's egg manioc | | Ny | y | | S |
| | | = *Ake* £ | B.301 | | | Ny | y | | S |
| | | = *Mutãngani* | | Manioc of the Whites | | MO, Ng | y | | S |
| | | = *Otãngani* (?) | | | | MO, Ng | y | | B |
| | | = *Timba Jaune* | | Yellow sweet manioc | | Ng | y | | S |
| 59 | *Didukuru* Δ | | B.41 | | | Ng | | | S |
| 60 | *Difubu* Δ | | B.41 | | | Ng | | | B |
| 61 | *Dikungu* | | | | | Ng | w | 6 | B |
| 62 | *Dilãndji* | | B.52 | | | OL | | | S |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 63 | *Dilolu* | | B.41 | Papaya (*Carica papaya* L., Caricaceae) | | Ng | | | S |
| 64 | *Dingoñe* | | | | | OI | | | B |
| 65 | *Dipumè* Δ | | B.21 | | | | | | S |
| 66 | *Ditadi Igulu* | | B.41 | Old Ditati | | Ng | | | S |
| 67 | *Ditoto* | | B.41 | *Musa* spp. | | Ng | w | 6 | S |
| 68 | *Djalabumi* | = *Djilabumi*, *Bvulabumi* | B.71 | Fills the belly | | HO | | | B |
| | | = *Djila Ossoli* (?) | B.71 | | | HO | | | B |
| 69 | *Djogo* | | B.71 | Elephant (*Loxodonta cyclotis* Matschie, Elephantidae) | | HO | | | B |
| | | = *Nzoghu* | B.11 | Variety of plantain with big fruits | | MO | | | B |
| | | = *Zôk* | A.85b | | | OI | | | B |
| | | = *Zoku* | A.85b | | | OI | | | |
| 70 | *Djuya* Θ | | A.75 | | | MO | | | ? |
| 71 | *Dukakaga* | | B.41 | Pangolin (*Manis tetradactyla* L., Manidae) | | Ng | w | | S |
| | | = *Likaga*, *Lekaga* | B.70 | | | HO | | | S |
| | | = *Ekaga* δ | | | | OI | | | |
| 72 | *Dûm* | = *Dõmb* (?), *Dume* Я, *Ndume* Я | A.85b | *Ceiba pentandra* Gaertn., Malvaceae | | OI | | | B |
| 73 | *Dussungubali* | | B.41 | (Fruit) | | Ng | | | S |
| 74 | *Ebaõnbomatari* δ | | | | | oI | | | |
| 75 | *Ebonia* δ | | | | | OI | | | |
| 76 | *Ecu* | | | | | Es | | | S |
| 77 | *Edam* | | | | | Ng | | | S |
| 78 | *Edodo* | | | | | Ng | | Y | S |
| 79 | *Eduima* | | | *Cylicodiscus gabunensis* Harms, Fabaceae (?) | | OI | | | |
| 80 | *Edu'u* ● | | B.11 | Old camp | Ga | OM | | | S |
| 81 | *Efouma* Θ | | B.11 | | | MO | | | ? |
| | | = *Efma* Θ | A.75 | | | MO | | | ? |
| 82 | *Egwèta* Δ | | B.31 | | | Ng | w | | S |
| 83 | *Ekolo'arendo* ● | | B.11 | (Village in Gabon) | Ga | MO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 84 | *Elãmbo* δ | | | | | OI | | | |
| 85 | *Elekõnd* | | | | | OI | | | |
| 86 | *Eliãmba* δ | | | | | OI | | | |
| 87 | *Emuõngo* | | | | | HO | | | B |
| 88 | *Entete* | | | | | HO | | | |
| 89 | *Epãndja* | | B.11 | Which destroys (?) | | OM | w | 12 | B |
| 90 | *Erikunda* | | | | | HO | | | B |
| 91 | *Esobo-Nku* | | A.75 | Salt burn | Ca | Ca, Eq, WT | w | 6,Y,s | B |
| 92 | *Esunge* | = *Esõnge* | B.11 | Hawk | | MO | | | B |
| 93 | *Etchinoku* | | | | | OI | | | |
| 94 | *Evizovizo* Θ | | B.11 | Magic | | MO | | | S |
| 95 | *Ewo* | | | | | HO | | | B |
| 96 | *Eziõng* | | A.75 | (Fern) | Ca? | OI | | | B |
| 97 | *Fala* | | | France | | HO | | | B |
| 98 | *Francine* ● | | | (Firstname) | Ga | OM | | | S |
| 99 | *Fufu* | | | (manioc-based dish) | | OL | w | | S |
| 100 | *Fula* | | | Black powder | | Ng | w | 12 | B |
| 101 | *Gebõnga* δ | | | | | OI | | | |
| 102 | *Geneviève* ● | | | (Firstname) | Ga | MO | | | B |
| 103 | *Gevee* Δ | | B.31 | | | Ng | | | B |
| 104 | *Gevima* Δ | | B.31 | | | Ng | | | B |
| 105 | *Ghibadungu* | | B.31 | Duck | | Ng | | | S |
| | | = *Otchaka* | B.31 | | | Ng | | | S |
| | | = *Dibutu* | B.43 | Vagina | | Ny | | | S |
| | | = *Gebadãngo* £ | B.301 | | | Ng | | | S |
| 106 | *Gimõngi* | | B.41 | The darkness | | Ng | w | 12 | B |
| | | = *Imõngi* | | | | HO | | | S |
| | | = *Imõngo* | | | | HO | | | B |
| 107 | *Gobatchika* | = *Lelãngeula* | B.52 | The one who bears earrings | | OL | w | | |
| 108 | *Gõndabite* Я | | | | | OI | | | S |
| 109 | *Ibibu* | | B.43 | Owl | | OM | | | B |
| 110 | *Ibola* | | B.31 | | | Ng | | | S |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 111 | *Idjõmba s'eliwa* ● | | B.11 | The wedding of the lake | Ga | MO | | | B |
| 112 | *Ighozo* Θ | | B.11 | *Setaria megaphylla* [Steud.] T., Dur. & Schinz, Poaceae | | MO | | | B |
| 113 | *Ikolõngo* | | A.75? | Dead trees | | MO | | | B |
| 114 | *Ikõndo* | | B.11 | Plantain (*Musa sapientum* var. *paradisiaca*) | | MO | | | B |
| 115 | *Ikwãmba* Θ | = *Akwãmba* Θ | B.11c | (Generic name for sweet manioc) | | MO | | | S |
| | | = *Dikwama* | | | | OL | | | S |
| 116 | *Iloti Nõmbe* | | B.11 | Black root | | OM | | | |
| | | = *Mpira Nõmbe* | B.11 | Dark coal or Gun powder; also the name of a variety of plantain | | OM | | 6 | S |
| 117 | *Inãnga* | | B.11 | | | OM | | | S |
| | | = *Anãnga* Я | A.85b | | | OI | | | S |
| 118 | *Inemempa* | | B.22 | | | OI | | | |
| 119 | *Ipãndo* Δ | | B.31, B.303 | | | Ng | | | S |
| | | = *Epãndo* Δ | B.11e | (Generic name for sweet manioc) | | OM | | | S |
| | | = *Dipãndo* | | (Generic name for sweet manioc) | | Ng | | | S |
| 120 | *Isamambu* | = *Isamambo* | B.52 | Looking for troubles | | OL | | w | S |
| 121 | *Iwãngo* Θ | | B.11c | | | MO | | | ? |
| 122 | *Kafula* | = *Kãmpfula* | B.71 | Waste | | HO | | | B |
| 123 | *Kaga Ãndala* | = *Kaga Ãndali* | B.71 | | | HO | | | B |
| 124 | *Kaioio* | | | (Lastname) | | HO | | | S |
| | | = *Okukuia* | | (Village in Congo) | | HO | | | S |
| | | = *Lãnduga* | B.71 | (Generic name for sweet manioc) | | HO | | | S |
| 125 | *Kãmi* | | B.71 | (Ant) | | HO | | | B |
| 126 | *Kãmpele* | | B.71 | (Lastname) | | HO | | | B |
| 127 | *Kãnga* | | B.71 | Partridge (*Guttera plumifera* Cassin, Numididae) | | HO | | | B |
| 128 | *Kãngole* Я | = *Kãngola* Я | | | | OI | | | B |
| 129 | *Kasibi* | | B.71 | Antelope (*Cephalophus leucogaster* Gray) | | HO | | | B |
| | | = *Kisibi, Isibi* | | | | HO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 130 | *Kikwo-Edzuwa* | | B.70 | Soft manioc | | HO | | | S |
| 131 | *Komo* Я | | | | | OI | | | B |
| 132 | *Kõnda* | | | Plantain (*Musa sapientum* var. *paradisiaca*) | | OL | | | B |
| 133 | *Kõngokolo* Я | | | | | OI | | | B |
| 134 | *Konõngo* | | | (Bird) | | HO | | | B |
| 135 | *Kopelitini* | = *Couverture* Я | | Blanket | | OI | | | S |
| | | = *Kupeletini* Я, Kupilitin Я | | | | OI | | | S |
| 136 | *Mboe* Δ | | A.75 | | Ca? | WT, Es? | | | S |
| 137 | *Kote* Я | = *Koto* Я | | | | OI | | | B |
| 138 | *Kubulu* | | | | | HO | | | B |
| 139 | *Kudie* Я | = *Kudi* Я, *Kudu* Я | | | | OI | | | S |
| 140 | *Kumba Mavungu* | | B.43, B.44 | | | OM | | | S |
| 141 | *Kundja* | | | | | HO | | | B |
| 142 | *Kungu* | | | | | HO | | | B |
| 143 | *Kunungu* | | | Little shrimp | | HO | | | B |
| 144 | *Kutu Bata* | | B.602 | A full basket | | HO | | | B |
| 145 | *Kwamakoss* Я | *Kwamukoso* Я, *Mukwamukoso* Я | | | | OI | | | B |
| 146 | *Kwapoto* Я | *Mukwapoto* Я, *Ukwapoto* Я | | | | OI | | | B |
| 147 | *Kwata Balumbu* | | | Kwata from the Balumbu | | Ng | | | B |
| 148 | *Kwata Igulu* | | | Old Kwata | | Ng | | | S |
| 149 | *Kwata Mayumba* | | | Kwata from Mayumba | | Ng, Ny | | | S |
| | | = *Moundjõmb* | | | | Ng | w | 12 | S |
| | | = *Mounzoumba* | | | | Ng | | | S |
| | | = *Modiõmbe* (?) | | | | Ng | | | S |
| 150 | *La Bière* | | | The beer manioc | | Ng | | | S |
| 151 | *Lambarene* | | | (City) | | MO | | | B |
| 152 | *Lãndi Lãndi* | | B.11 | Long manioc | | OM | w | 12 | B |
| | | = *Lãnga Lãnga* | | | | OM | | | B |
| | | = *Lãndeleuleu* | B.41 | | | OL | | | B |
| 153 | *Lãngori* | | B.71 | Something free (?) | | HO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 154 | *Laurence* ● | | | (Firstname) | | MO | | | B |
| 155 | *Leboyo* | | B.70 | | | HO | | | B |
| 156 | *Ledjãnga* | = *Dinjãnga* | B.52 | | | OL | | | S |
| | | = *Dinzãnga* | B.43 | | | Ny | | | S |
| | | = *Mãndjãnga* Δ (?) | B.304 | | | Ng | | | B |
| | | = *Ndjãnga* Δ | B.11e | | | OM | | | S |
| | | = *Endjãnga* Δ | B.31 | | | Ng | | | S |
| | | = *Dintsãnga* Δ | B.41 | | | Ng | | | S |
| | | = *Ndjãnga* Δ | B.62 | | | HO | | | S |
| | | = *Enzãnga* £ | B.301 | | | Ng | | | S |
| 157 | *Leghagheula* | | B.52 | Pangolin (*Manis tetradactyla* L., Manidae) or *Tetracera alnifolia* Willd., Dilleniaceae | | OL | | | S |
| 158 | *Lekaga Mopini* | | B.70 | Black pangolin (*Manis tetradactyla* L., Manidae) | | HO | | | B |
| 159 | *Lekõndo* | | | Plantain (*Musa sapientum* var. *paradisiaca*) | | HO | | | S |
| 160 | *Lekuna* | | | (Village in Congo) | Co | HO | | | B |
| 161 | *Lepungu* | | B.52 | Umbrella manioc or Bat (Mammalia, Chiroptera) | | OL | (2) | | S |
| | | = *Farine* | B.71 | Flour manioc | | HO | | | S |
| 162 | *Lingala* | | C.30b | Manioc of the Lingala | Co | MO | | | S |
| 163 | *Loulou* ● | | | (Firstname) | | MO | | | B |
| 164 | *Lungayuwe* | | B.77 | | | HO | | | B |
| 165 | *Maboundi* | | B.31 | | | Ng | | | S |
| 166 | *Maboundinieghe* | | B.31 | | | Ng | | | S |
| 167 | *Madame Wani* | = *Luanda, Maya* | | (Lastname) | | OM | w | 8 | B |
| 168 | *Madouedoue* | | B.11 | | | OM | | | S |
| 169 | *Mafuta Mãngo* | | B.70 | The lie of the panther | | HO | | | B |
| 170 | *Makwaka* | | B.70 | | | HO | (2) | | B |
| 171 | *Malege* | | | Small bumps manioc | | HO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 172 | *Mamamaboul* δ | | | | | OI | | | |
| 173 | *Mãmbia* | | | | | HO | | | B |
| | | = *Mãmbia* | | | | OL | | | S |
| 174 | *Mana* | | B.11a, B.31 | To finish | | Ng | w | 12 | S |
| 175 | *Mãndale* Я | | | | | OI | | | S |
| 176 | *Mãndjogo* | | | | | OM | | | |
| 177 | *Mangemvu* | | | (Lastname) | | Ng | | | S |
| 178 | *Mãngwala* | | | | | OI | | | B |
| 179 | *Maniebwe* Я | = *Maniebo* Я | | | | OI | | | S |
| 180 | *Marcelline* | | | (Firstname / not the original name) | | OM | | | B |
| 181 | *Marchandise* Я | | | | | OI | | | B |
| 182 | *Marron* | | | Brown manioc | | OM | | | B |
| 183 | *Masãndouce* Я | | | | | OI | | | S |
| 184 | *Matad*[3]*i* Ψ,Θ,δ | | A.75, B.11a,b,c | (Harbour in Congo) | | Es, OM, MO, Ng, OI | w | 8 | S |
| | | = *Litedi* | | | | OL | | | S |
| | | = *Ditadi* | | | | Ng | | | S |
| | | = *Etadi* £ | | | | Ng | | | S |
| | | = *Ogelo* | | | | OM | | | S |
| 185 | *Matali* Я | | | | | OI | | | S |
| 186 | *Matchakara* | | | Small foot manioc | | HO | | | B? |
| 187 | *Matsamara* | | | | | HO | | | B? |
| 188 | *Mazãnga* Я | = *Mazãngue* Я | | | | OI | | | S? |
| 189 | *Mazara* Я | | | | | OI | | | S |
| 190 | *Mbaombaõn* δ | | | | | OI | | | ? |
| 191 | *Mbèno* Δ | | B.21 | | | | | | B |
| 192 | *Mbikini* | = *Mumbikini* | B.43? | | | Ng | | | B |
| 193 | *Mbong-Ndama* | = *Ndama* | A.75 | | | Es | | | B |
| 194 | *Mbulanagãndo* | | B.41 | | | Ng | w | 8 | S |
| 195 | *Mbulu* | | | Seed manioc | | OL | | | B |
| 196 | *Mbutu* | | | (Fish) | | HO | | | S |
| 197 | *Mbwasia* | = *Mbwasie* Я, *Bwasie* Я | | | | OI | | | S |

[3] Sent in the 1920s to Libreville to Mgr. Martrou by R.F Justin Gillet, curator of the botanic gardens of Kisantu, in DR Congo.

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 198 | *Medzim-Meyõng* Δ | | A.75 | | | WT, Es? | | | S |
| 199 | *Mèkulu-Mè-Mbelo* Δ | | B.21 | Pink flamingo legs manioc | | WT, Es? | | | S |
| 200 | *Mesimesa* Я | | | | | OI | | | S |
| 201 | *Moabi* Δ | = *Oabe* Δ | | *Mimusops djave* Laness. ex Engl., Sapotaceae | | Ng | | | S |
| | | = *Wabe* £ | B.301 | | | Ng | | | S |
| 202 | *Mogèkè* Δ,£ | | B.31,B.301 | | | Ng | | | S |
| 203 | *Mogènda* Δ,£ | | B.31, B.304 | | | Ng | | | B |
| 204 | *Monseigneur* | | | Lord | | Ng | | | S |
| 205 | *Mõnzano* Θ | | A.75 | | | MO | | | ? |
| 206 | *Moponia* δ | | | | | OI | | | B |
| | | = *Mopini* | | Black manioc | | HO | | | B |
| | | = *Õnpini* | | | | HO | | | |
| 207 | *Moulimagnama* | | | The perfect side dish for meat | | HO | | | B |
| | | = *Olimagnama* | | | | HO | | | B |
| 208 | *Moumãngo* | | | | | HO | | | B |
| 209 | *Moungebe* | | | Small manioc | | HO | | | I |
| 210 | *Moungwa Basenge* | | | The salt of the Basenge | | HO | | | B? |
| 211 | *Mounienzebolo* | | | *Amaranthus* spp. | | HO | | | S |
| 212 | *Mountzãnga* | | | | | HO | | | B |
| 213 | *Mouyika* | | | Taro (*Colocasia esculenta* [L.] Schott, Araceae) | | HO | | | S |
| 214 | *Moyiding* | | | | | HO | | | B |
| 215 | *Mpindo* Δ | | B.21 | | | | | | B |
| 216 | *Mpiza-Vizue* | | B.11 | Zigzag manioc | | MO | | | S |
| 217 | *Mpongwe* | | B.11a | Manioc of the Mpongwe | | MO | | | B |
| 218 | *Mubõngo* | | | | | HO | | | ? |
| 219 | *Mugumbu* | | | | | Ng | w | | S |
| 220 | *Mugwendje* Я | | A.85b | | | OI | | | S |
| 221 | *Mukãngi* | = *Mukãnga* | | | | HO | | | B |
| 222 | *Mukeki* | | | | | Ng | | | S |
| 223 | *Mukuaku* | | | | | Ng | | | |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 224 | *Mukuma* | | | *Ceiba pentandra* Gaertn., Malvaceae | | OL | | | B |
| 225 | *Mumeni* | | | Manioc which grows on its own | | HO | | | B |
| 226 | *Munãnga* | | | | | OL | | | B |
| 227 | *Munughubiogho* | | B.52 | Broken foot manioc | | OL | | | S |
| 228 | *Mupala* | | | Plantain (*Musa sapientum* var. *paradisiaca)* | | Ng | | | S |
| 229 | *Mupele* | | B.28 | | | HO | | | B |
| | | = *Opele* | B.62 | | | HO | | | |
| | | = *Wakwãngugu* | | Manioc which has lost its mother | | HO | | | B |
| | | = *Wokwãngugu* | B.602 | | | HO | | | B |
| | | = *Wakwãngu* | | Manioc which has its mother | | HO | w | | B |
| | | *Gãngugu* | B.602 | Manioc which has its mother | | HO | | | B |
| 230 | *Mupwena* | | | | | OI | | | |
| 231 | *Mussala* | = *Mossala* | | | | HO | | | B |
| 232 | *Musungu* | | | Sugarcane (*Saccharum officinarum* L., Poaceae) | | HO | | | S |
| 233 | *Muteli* | | | | | Ng | w | 12 | S |
| 234 | *Muteti* | | | Three or trade (in Mpongwe B.11a) | | HO | | | S |
| 235 | *Mutõmbi* | *Motõmbi* | B.31 | *Copaifera religiosa* J.Leonard, Caesalpiniaceae | | Ng | (2) | 12 | B |
| | | *Etumbi* Δ | B.62 | | | HO | | | B |
| 236 | *Mutuki* | | | Variety of plantain with purple fruits | | Ng | | | B |
| 237 | *Muvovodi* | *Mupopodi* | | *Treculia acuminata* Baill., Moraceae | | OL | | | S |
| 238 | *Muwivu* | | | (Lastname) | | OM | | | B |
| 239 | *Mwagãnga* | | | The son of the fetish maker | | HO | | | S |
| 240 | *Mwatãnga* | | | The child of the White | | OI | | | S |
| | | *Mwaitambãnge* Я (?) | | | | OI | | | |
| 241 | *Mwatebadzila* | | B.70 | A strong woman | | HO | | | B |
| 242 | *Mwèbwè* | | | | | OI | | | |
| 243 | *Mwoso* | | | | | OI | | | |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 244 | *Ndimina* | | B.11 | (Lastname) | | OM | | 6 | S |
| 245 | *Ndina* | | B.11 | *Swartzia fistuloides* Harms, Fabaceae | | MO | | | B |
| 246 | *Ndjiabogo* Δ | | B.62 | | | HO | | | B |
| 247 | *Ndongè ya pupu* Δ | | B.11a | | | OM | w | | S |
| 248 | *Ndongè ya tatena* Δ | | B.11a | | | OM | p | | S |
| 249 | *Ndumbula* Δ | | B.11e | | | OM | | | S |
| 250 | *Ndungu* | | | *Fagara heitzii* Aubr. et Pellegr., Rutaceae | | Ng | w | 12 | B |
| 244 | *Ndimina* | | B.11 | (Lastname) | | OM | | 6 | S |
| 245 | *Ndina* | | B.11 | *Swartzia fistuloides* Harms, Fabaceae | | MO | | | B |
| 246 | *Ndjiabogo* Δ | | B.62 | | | HO | | | B |
| | | = *Ndõng* | A.75 | | | Ng | w | 12 | B |
| | | = *Ndõngo* £ | B.301 | | | Ng | | | B |
| 251 | *Ndungu Igulu* | | | Old Ndungu | | Ng | | R | B |
| 252 | *Ndza Bouane* | | B.22 | | | MO | | | B |
| 253 | *Ndzao Re Bimbia* | | B.11 | | | Ng | w | 12 | B |
| | | = *Ndzao Re Bimbi* | B.41 | | | OM | | | B |
| | | = *Ndjawebimbia* | B.43 | | | OM | | | |
| | | = *Mõngiloti* | B.11 | Sweet potato manioc | | OM | | | B |
| | | = *Ngungu Remba* Θ | A.75, B.31 | | | Ng | | | B |
| | | = *Digõndi* | B.11 | (Lastname) | | OM | | | B |
| | | = *Oguka* | B.11 | | | OM | | | |
| | | = *Rizõmbo* | B.11 | | | OM | | | |
| | | = *Karonari* | B.11 | | | OM | | | |
| 254 | *Ngãnda* | = *Ngãndo* | | | | HO | | | B |
| 255 | *Ngonono* | | B.71 | Hard | | HO | | | B |
| 256 | *Ngulu Mukasa* | | | | | HO | | | B |
| 257 | *Ngumba* | = *Ngõmba* | | Porcupine (*Atherurus africanus* Gray, Hystricidae) | | OL | w | | S |
| 258 | *Ngungu* | | | | | HO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 258 | *Ngungu* | | | | | HO | | | B |
| 259 | *Ngu'u* | | | Hippopotamus (*Hippopotamus amphibius* L., Hippopotamidae) | | MO | | | B |
| 260 | *Nguya* | | | Bush pig (*Potamochoerus porcus* L., Suidae); also name of a variety of plantain | | Ng | | | S |
| | | = *Ngoya* | | | | Ng | w | | S |
| | | = *Nguya Mudzaka* | | | | HO | | | S |
| | | = *Nguya* | | | | HO | | | B |
| 261 | *Ngwekyakya* Θ | | | | | MO | | | |
| 262 | *Ngweli* | | | Partridge (*Guttera plumifera* Cassin, Numididae) or "The | | OL | | | S |
| 263 | *Ngwesuku* ●,Ψ | | B.11 | (Lastname) | | OM | w | 6 | B |
| 264 | *Nièniè* | | | | | HO | | | B |
| 265 | *Nkala* Δ | | B.62 | | | HO | | | B |
| 266 | *Nkèn-Ogogo* Δ | | A.75 | | | WT, Es? | | | B |
| 267 | *Nkõnga* Δ | | B.11e | | | OM | | | S |
| 268 | *Nkot-Mbõng* | | A.75 | Dry manioc | | WT | w | 6,R | B |
| 269 | *Nkoula-Nõmbe* | | B.11 | Black nut | | MO | | | B |
| 270 | *Nkunungu* Δ | | B.62 | | | HO | | | B |
| 271 | *Ntaba* | | | Goat (*Capra aegagrus hircus* L., Bovidae) | | HO | | | B |
| 272 | *Ntchagi Modju* | = *Ntchagimikami* | | Narrow leaves manioc | | HO | | | B |
| 273 | *Ntse Putu* Θ | | B.11c | Portugal | ST | MO | | | B |
| 274 | *Ntselele* | | | (Termite) | | OM, MO | w | 12 | B |
| 275 | *Ntséndé* Δ | | B.21 | | | | | | B |
| 276 | *Ntsumu* ● | | | Manioc seedling | | OM | | | B |
| 277 | *Nwoni* | = *Nioni* | | (Bird) | | HO | | | B |
| 278 | *Nyènghè* Δ | | B.62 | | | HO | | | B |
| 279 | *Nzengui* ● | | | (Lastname) | | MO | | | S |
| 280 | *Oba* Δ | | B.11a | | | OM | | | S |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 281 | *Obaba* | | B.71 | Red | | HO | | | S |
| 282 | *Obagãmpali* | | B.71 | Who finds the strength (?) | | HO | | | B |
| 283 | *Obiri* | | B.71 | (Fish) | | HO | | | B |
| 284 | *Obuga Obvula* | | B.71 | Who exceeds the family's needs (?) | | HO | | | B |
| 285 | *Obve Akema* | | B.71 | | | HO | | | B |
| 286 | *Ochemi* | | B.71 | (Bird) | | HO | | | B |
| 287 | *Ofufu* | | B.71 | White (?) | | HO | | | B |
| 288 | *Oghoa* | | B.11 | Yellow manioc | | MO | (2) | | S |
| 289 | *Ognana* | | B.71 | | | HO | | | S |
| 290 | *Ogoumapobi* δ | | | | | OI | | | |
| 291 | *Ogulungu* | | B.11 | (Bird) | | MO | w | 6 | S |
| | | = *Ogurungu, Pinde* | B.11 | | | OM | | | B |
| | | = *Pinda* | | Black manioc (?) | | OL | | | B |
| 292 | *Oielekunda* | | B.71 | A smart choice | | HO | | | B |
| 293 | *Okari Kabvula* | | B.71 | Who overtakes others | | HO | | | B |
| 294 | *Okari Kabvula* | = *Okari Kakara?* | B.71 | A skinny woman | | HO | | | B |
| 295 | *Okuma* Δ | | B.62 | | | HO | | | S |
| | | = *Kuma* Я (?) | A.85b | | Ca | OI | | | B |
| | | = *Kume Kume* Я (?) | | | Ca | OI | | | B |
| | | = *Kuluma* β | A.85b | | Ca | OI | | | |
| 296 | *Okunda* | | B.71 | (Village in Congo) | Co | HO | | | B |
| | | = *Okundza* δ | | | | OI | | | |
| 297 | *Okwata* | | B.11? | (Lastname) | | OM, MO, Ng, OI? | | | S |
| | | = *Kwata* £ | B.301 | | | Ng | | | S |
| 298 | *Olaloa* | | B.11 | | | MO | | | |
| 299 | *Õmboma* | | B.11 | Boa (*Python sebae* Gmelin, Pythonidae) | | OM | w | 6 | B |
| | | = *Mboma* | | | | Ng | | | S |
| | | = *Mbomo* | | | | HO | (2) | | B |
| | | = *Bãmboma* δ | | | | OI | | | |
| 300 | *Omonoiemi* | | B.71 | A pregnant woman | | HO | | | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 301 | *Õndzalapaki* | | B.71 | Who eases hunger quickly | Co | HO | | | S |
| | | = *Mõndjelepako* Я | | | Co | OI | | | S |
| | | = *Mõndjelepaku* Я | | | | OI | | | S |
| 302 | *Õngele* | | B.71 | (Lastname) | | HO | | | B |
| 303 | *Onindi* ● | | B.11 | (Lastname) | | MO | | | B |
| 304 | *Õnjabi* | | B.52 | Manioc of the Ndzabi | | HO | | | B |
| 305 | *Õntchitcheli* | | B.71 | (Insect) | | HO | | | B |
| 306 | *Opipi* | | B.71 | Black manioc | | HO | | | B |
| 307 | *Opupu* | | B.71 | White manioc | | HO | | | B |
| 308 | *Osabege* | | B.71 | (Village in Gabon) | | HO | | | B |
| 309 | *Ossamouédembo* ● | | B.11 | (Village in Gabon) | | MO | | | B |
| 310 | *Ossãngala* | = *Kassãngala, Ãngala* | B.71 | (Village in Gabon) | | HO | | | B |
| 311 | *Ossewa* | | B.11 | | | MO | | | S |
| 312 | *Ossoele* | | | (Village in Gabon) | | HO | | | B |
| 313 | *Otuo Bata* | | B.62 | | | HO | | | B |
| 314 | *Owãntope* | | B.11 | A small woman | | OM | w | 12 | B |
| 315 | *Oyagija* | | B.71 | Long-awaited manioc (?) | | HO | | | B |
| 316 | *Oyogho* Θ | | B.71 | A honest man | | MO | | | B |
| 317 | *Ozãmbi Bakõngo* Θ | | A.75 | | | MO | | | ? |
| 318 | *Pana* | | | (Village in Congo) | Co | HO | | | B |
| 319 | *Pãndinu* | | B.22 | | | OM | | | S |
| 320 | *Pauline* Θ,Я ● | | B.71, B.11c, B.31, B.602, B.28, B.23, B.62, B.77, B.73a, B.71 | (Firstname) | | MO, Ng, HO | | | S |
| 321 | *Pepe* | | | | | HO | | | B |
| 324 | *Pokwe* | | A.85b | | | OI | | | B |
| 322 | *Pidje* Я | = *Tatu* Я | | | | OI | | | S |
| 323 | *Piupiu* | = *Mopiupiu* | | | | HO | | | B |
| 324 | *Pokwe* | | A.85b | | | OI | | | B |
| 325 | *Premier Choix* | | | First choice manioc | | MO, OM | w | 12 | B |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 325 | *Premier Choix* | = *Monãnzabe* | B.31, B.301, B.304, B.305 | God's child | | Ng | | | |
| 326 | *Punge* Δ | | B.31 | | | Ng | | | S |
| 327 | *Putu* Δ,Ψ,Θ | | B.11b,c,e | | | OM, MO, Ng, OI? | | | B |
| | | = *Puta* | B.41 | Manioc of the Portuguese | | Ng | w | 12 | B |
| | | = *Putu-Bakõngo* | B.11b | | | MO | | | B |
| | | = *Putsu* Δ | B.21 | | | | | | B |
| 328 | *Regholoto* Θ | | B.11c | | | MO | | | B |
| 329 | *Samkita* | | | (Village) | | MO | | | B |
| 330 | *São Tomé* | | ST | | | Ng | w | 12 | S |
| 331 | *Simambõndo* | | | | | HO | | | S |
| 332 | *Simbu* | | B.43? | | | Ng, Ny? | | | S |
| 333 | *Singana* | | | Don't try to do the same | | Ng | | Y | B |
| 334 | *Six Mois* | | | Six months manioc | Co | HO | w | 6 | S |
| | | = *Sãnza Motuba* | C.30b | | | HO, OI | | | B |
| | | = *Sanyamotoba* Я, *Sayanatoba* Я | | | | OI | | | |
| | | = *Õngania* | B.71 | | | HO | | | B |
| | | = *Ungañinga* | | | | OI | | | B |
| 335 | *Syèlili* Δ | | B.41 | | | Ng | | | B |
| 336 | *Tambroussi* | | B.11 | Wake me up | | OM, Ng | | | S |
| 337 | *Tãnga* | | | | | HO | | | |
| 338 | *Telatela* | | | | | OI | | | |
| 339 | *Tia* ● | | B.11 | (Lastname) | | MO | | | B |
| 340 | *Timbendule* | | B.31 | Black root (?) | | Ng | | | B |
| | | = *Ndule* Я (?) | | | | OI | | | B |
| 341 | *Tõngomokwa* | | | | | OI | | | B |
| 342 | *Totomavemi* | | B.11 | I might be wrong | | OM | w | 12 | S |
| 343 | *Trente-trois* | | | Lambarene PK 33 | | Ng | w | 8 | S |
| 344 | *Tsete* | | | Arrow | | HO | | | B |
| 345 | *Tulu* Δ | | B.41 | | | Ng | | | B |
| 346 | *Uvina* Δ | | B.21 | | | | | | S |

| | Landrace[a] | Alternative name(s) | Language(s) | Translation | Origin[b] | Distribution[c] | Characteristics | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Morph[d] | Agro[e] | Orga[f] |
| 347 | *Vaga* | | | (Village in Congo) | Co | HO | | | B |
| 348 | *Vidèko* Δ | | B.21 | | | | | | S |
| 349 | *Vidi* Δ | | B.21 | | | | | | S |
| 350 | *Visoso* £ | | B.301 | | | Ng | | | S |
| 351 | *Yabolo* Θ | | A.75 | | | WT? | | | ? |
| 352 | *Yala* | | B.52 | | | OL | w | | B |
| 353 | *Yamouge* | | A.75 | | | MO | | | B |
| 354 | *Yetenambõngue* Я | = *Yetenambõngo* Я | | | | OI | | | B |
| | | = *Djeyetenambõngue* Я | | | | OI | | | S |
| | | = *Djeyetenambõngue* Я | | | | OI | | | S |
| 355 | *Zibu* | | | | | OI | | | S |

# Supplementary analyses

# C1. Genetic analyses

## Methods

*DNA extractions.* DNA extractions were performed on 20mg of dried leaves, using DNeasy ® Plant Mini kits (Qiagen ®) and following the manufacturer's recommendations. Purified DNA was eluted in a final volume of 200µl. The quality of the DNA extraction was checked via gel electrophoresis. Six µl of template from twenty-four randomly chosen samples were loaded together with 2µl of loading dye on 1.5% agarose gel (1.5g agarose, 100ml TBE buffer, 4µl EtBr) in Tris: Boric acid: EDTA (TBE) buffer (0.445M Tris-HCl, 0.445M Boric acid, 0.055M disodium EDTA, pH 8.3). The gel was run at 145V for 20 minutes, then visualized under a UV light source. DNA concentration and purity were checked using an Eppendorf ® BioPhotometer. Measurements were taken from 30 randomly chosen samples. DNA final concentration was between 0.015 and 0.15µg/µl, with an A260/A280 purity ratio of 1.7-1.9.

*PCR amplifications.* Polymerase chain reactions (PCR) were performed using Qiagen® Multiplex PCR kits and phosphoramidite-labeled primers (MWG Biotech, Ebersberg, Germany). To ensure unambiguous peak assignment, primer pairs were pooled in two different sets (M5·1 and M5·2) as described in Table C1.1. Primers were re-suspended in TE buffer (10mM Tris·Cl, 1mM EDTA, pH 8.0) and normalized to a 100µm (100pmol/ul) stock solution. For each set, a 10x primer mix containing each primer at 2µM was prepared adding 10µl of each primer stock solution to sterile ultra-pure water for a final volume of 500µl. All amplifications were carried out on a Biometra® TProfessional 96-well gradient thermal cycler. PCR amplifications were performed in a final volume of 10µl on 96-well PCR plates (Sarstedt AG&Co). Amplification conditions followed the Qiagen protocol. Along with 1µl of non-diluted DNA template, each well contained 5µl of 2x Qiagen Multiplex PCR master mix, 1µl of 10x primer mix (whether M5·1 or M5·2) and 3µl of RNase-free water, in compliance with the 1:1 kit/primer ratio recommended by Qiagen. An initial activation step at 95°C for 15 minutes preceded 30 cycles of amplification, starting with an annealing step of 90 seconds at 55°C, and continuing with an extension at 72°C for one minute. Amplification ended with a final extension at 60°C for half an hour.

**Table C1.1. Composition of the two primer sets, M5·1 and M5·2**, with predicted size range (in bp).

| | Primer | Size range | Annealing T° | Label | Colour |
|---|---|---|---|---|---|
| M5·1 | GAGG5 | 110-130 | 56°C | TAMRA | Yellow |
| | GA21 | 85-110 | 56°C | JOE | Green |
| | GA57 | 135-175 | 56°C | FAM | Blue |
| | GA126 | 160-210 | 56°C | JOE | Green |
| | GA134 | 305-340 | 56°C | FAM | Blue |
| M5·2 | GA12 | 115-145 | 56°C | JOE | Green |
| | SSR31 | 150-195 | 55°C | TAMRA | Yellow |
| | SSR55 | 110-135 | 55°C | FAM | Blue |
| | SSR68 | 225-290 | 55°C | FAM | Blue |
| | SSR169 | 80-110 | 55°C | TAMRA | Yellow |

*Genotyping.* Genotyping was performed on a 16-capillary AbiPrism™ 3130XL Genetic Analyzer (Perkin Elmer/Applied Biosystems®, Foster City, CA, USA). Each sample was prepared from 1µl PCR template (diluted 50x) to which 15µl formamide and 0.2µl GENESCAN™ 400 LIZ™ size standard (Applied Biosystems®) were added. To ensure comparability of data, a selection of samples from the previous batches was run together with every batch of samples. Genotypes were extracted and analysed using GENESCAN analysis® 3.1.2 software (Applied Biosystems®). To reduce the risk of typing errors, genotypes were controlled by checking allele peaks by eye.

*Genotyping errors.* Errors can arise in studies using fresh DNA, where primer-site mutations may result in non-amplified alleles (null alleles*), or where PCR artefacts can cause large allele drop-out* (*i.e.*, short allele dominance) or stutter bands*. Such errors can cause deviations from Hardy-Weinberg equilibria, and may bias population genetic analyses, but can easily be overcome. Loci often show consistent stutter patterns, and manual scoring was possible with relatively high confidence.

**Table C1.2. Repeat motif and sequences** (L: left, R: right) **of the 10 SSR nuclear primer pairs** used for the analyses, reproduced from [a] Chavarriaga-Aguirre *et al.* (1998) and [b] Mba *et al.* (2001).

| | Locus | Repeat motif | Primer 5' to 3' sequences |
|---|---|---|---|
| M5·1 | GAGG5 [a] | $(GAGG)_n$ | L. TAATGTCATCGTCGGCTTCG<br>R. GCTGATAGCACAGAACACAG |
| | GA21 [a] | $(GA)_n$ | L. GGCTTCATCATGGAAAAACC<br>R. CAATGCTTTACGGAAGAGCC |
| | GA57 [a] | $(GA)_n$ | L. AGCAGAGCATTTACAGCAAGG<br>R. TGTGGAGTTAAAGGTGTGAATG |
| | GA126 [a] | $(GA)_n$ | L. AGTGGAAATAAGCCATGTGATG<br>R. CCCATAATTGATGCCAGGTT |
| | GA134 [a] | $(GA)_n$ | L. ACAATGTCCCAATTGGAGGA<br>R. ACCATGGATAGAGCTCACCG |
| M5·2 | GA12 [a] | $(GA)_n$ | L. GATTCCTCTAGCAGTTAAGC<br>R. CGATGATGCTCTTCGGAGGG |
| | SSR31 [b] | $(GA)_{21}$ | L. CTTCATCACGTGTTAATACCAATC<br>R. ATTGTTGTGGTTGCAGGACA |
| | SSR55 [b] | $(GA)_{16}$ | L. GCAATTTGCAAAGACATACCA<br>R. TGTGGAGCTTGATTTTGCAG |
| | SSR68 [b] | $(CT)_{12}CC(CT)_{17}$ | L. GCTGCAGAATTTGAAAGATGG<br>R. CAGCTGGAGGACCAAAAATG |
| | SSR169 [b] | $(GA)_{19}A_3(GAA)_2$ | L. ACAGCTCTAAAAACTGCAGCC<br>R. AACGTAGGCCCTAACTAACCC |

n number of repeats.

# C2. SSR markers resolving power

## Methods

Fregene *et al.* (2003) established that below 30 unliked SSRs markers, one cannot span all information on genotypic diversity. The number of markers used for the genetic part of this thesis (10) might thus seem inadequate, but it was actually sufficient to assess most of the diversity present in Gabon, and proved to have a high resolving power.

*Relationship between SSR markers and genotypic diversity*. In order to check whether the set of markers used for the study permitted an accurate descriptions of the genetic diversity of manioc populations, MULTILOCUS 1.2 (Agapow & Burst 2001) was used to plot the genotypic diversity against the number of combined SSRs markers (Arnaud-Haond *et al.* 2005), without repeated MLGs (7 villages, 289 MLGs). The curve reached an asymptotic plateau over 7 loci, showing that adding more markers would not have significantly increased the resolution of genotypic diversity (Figure C2).

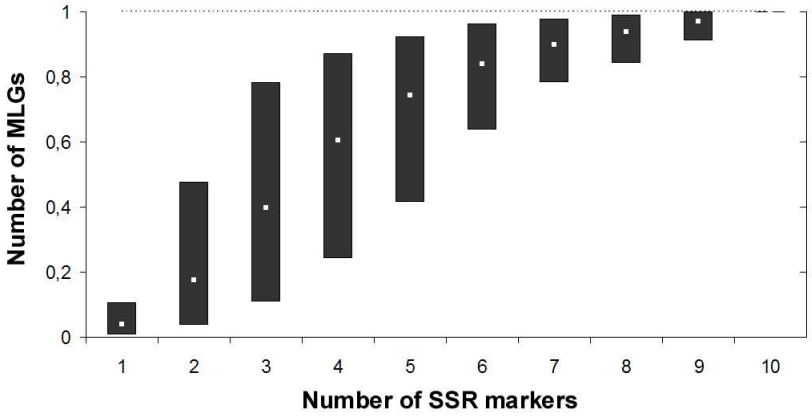



**Figure C2.** Curves describing the genotypic resolution of microsatellites, based on analysis of all possible combinations $C_n^l$ of *n* loci (*n* = 1,...,*l*; *l* = number of loci available), giving the average clonal richness *R* (±SE) for each *n*. Clonal diversity was estimated by $R = (G-1)/(N-1)$, where *G* is the number of genotypes (MLG) and *N* is the sample size.

# C3. Allelic diversity

**Table C3. Comparison of the alleles detected in Gabon** and those identified in other studies of manioc diversity in Africa, South America, and Asia, for the 10 markers used in the study. No comparative data are available for the locus SSR31. Data taken from the literature: [a] Elias *et al.* (2004), [b] Duputié *et al.* (2009b), [c] Elias *et al.* (2001a), [d] Chavarriaga-Aguirre *et al.* (1999), [e] Mkumbira *et al.* (2003). Alleles are coded with numbers, with the numbers referring to the allele's size (in base pairs) by increasing order. Codes are those used for describing the multilocus genotypes (MLG) identified in the three case studies presented in Chapters III, IV and V. Only alleles detected in Gabon were coded. Note that the allele lengths reported in the different studies may vary for a few bp. The values reported here are homogenized over the different studies, using the allele lengths from Gabon as the reference.

**GAGG5**

| Allele | 112 | 114 | 123 |
|---|---|---|---|
| Code | — | 1 | 2 |
| **Country** | | | |
| Brazil[a] | x | x | x |
| French Guiana[b] | | x | x |
| Gabon | | x | x |
| Guyana[c] | x | x | x |

**GA21**

| Allele | 104 | 106 | 108 | 110 | 112 | 114 | 116 | 118 | 120 | 122 |
|---|---|---|---|---|---|---|---|---|---|---|
| Code | — | — | — | 1 | 2 | — | — | 3 | — | — |
| **Country** | | | | | | | | | | |
| Argentina[d] | | | | | | x | x | x | | |
| Bolivia[d] | | | | | | x | x | | | |
| Brazil[a,d] | | x | x | x | x | x | x | x | x | x |
| China[d] | | | | | x | x | x | x | | |
| Colombia[d] | | | | | | x | x | x | x | x |
| Costa Rica[d] | | | | | | x | x | x | x | x |
| Cuba[d] | | | | | | x | x | | | |
| Dominican Republic[d] | | | | | | x | | | | |
| Ecuador[d] | | | | | x | x | x | | | x |
| Fiji[d] | | | | | | x | x | | | |
| French Guiana[b] | x | | | x | x | | | x | | |
| Gabon | | | | x | x | | | x | | |
| Guatemala[d] | | | | | | x | x | x | | x |
| Guyana[c] | x | | | x | x | x | | | | x |
| Indonesia[d] | | | | | | x | x | | | x |
| Malaysia[d] | | | | | | x | x | x | | x |
| Mexico[d] | | | | | x | x | x | x | | x |
| Nigeria[d] | | | | | | x | x | | | x |
| Panama[d] | | | | | x | x | x | | | x |
| Paraguay[d] | | | | | | x | x | x | | |
| Peru[d] | | | | | x | x | x | x | x | x |
| Philippines[d] | | | | | | x | x | | | |
| Puerto Rico[d] | | | | | | x | x | | | |
| Thailand[d] | | | | | x | x | x | | | x |
| USA[d] | | | | | | x | x | | | |
| Venezuela[d] | | | x | | | x | x | | | x |

**Table C3.** (continued)

**GA57**

| Allele Code | 156 1 | 160 — | 162 2 | 178 — | 181 3 | 183 — | 185 4 |
|---|---|---|---|---|---|---|---|
| **Country** | | | | | | | |
| French Guiana[b] | | | x | | x | x | x |
| Gabon | x | | x | | x | | x |
| Malawi[e] | | x | | x | | x | |

**GA126**

| Allele Code | 159 — | 181 — | 183 1 | 185 2 | 187 — | 189 3 | 191 4 | 193 — | 213 — | 216 5 | 217 — | 222 6 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Country** | | | | | | | | | | | | |
| Argentina[d] | | | | x | x | | x | | | | | |
| Bolivia[d] | | | | x | | | | x | | | x | |
| Brazil[a,d] | | x | | x | x | x | x | x | | x | x | x |
| China[d] | | | | x | | | | | | | x | |
| Colombia[d] | | x | | x | | x | x | x | | x | x | x |
| Costa Rica[d] | | | | x | x | | x | x | | x | x | x |
| Cuba[d] | | x | | x | | | x | x | | x | x | x |
| Dominican Republic[d] | | x | | x | | | | | | | | |
| Ecuador[d] | | x | | x | x | | | x | | x | x | |
| Fiji[d] | | | | x | | | | | | | | |
| French Guiana[b] | x | | x | x | x | | | | | | | |
| Gabon | | | x | x | | x | x | | | x | | x |
| Guatemala[d] | | | | x | | | x | x | | | x | |
| Guyana[c] | | x | | x | x | | x | x | | x | | |
| Indonesia[d] | | | | x | | | | | | | x | |
| Malaysia[d] | | | x | x | | | | | | x | | x |
| Malawi[e] | | | | x | x | | | | | x | | x |
| Mexico[d] | | | | x | x | | x | x | | | x | |
| Nigeria[d] | | x | x | x | x | | x | x | | x | x | |
| Panama[d] | | x | | | x | x | | | | | | |
| Paraguay[d] | | x | | | x | | | x | | | x | |
| Peru[d] | | x | | x | x | | x | x | x | | x | |
| Philippines[d] | | x | | x | x | | x | x | | | x | x |
| Puerto Rico[d] | | | | x | | | | x | | | x | |
| Thailand[d] | | | | x | | | | x | | | x | |
| USA[d] | | | | x | x | | | | | | x | |
| Venezuela[d] | | | | x | x | | | x | | | x | |

**Table C3.** (continued)

**GA134**

| Allele | 307 | 309 | 311 | 313 | 315 | 317 | 319 | 321 | 323 | 325 | 327 | 329 | 331 | 335 | 337 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Code | 1 | — | — | — | — | 2 | — | — | — | 3 | — | — | — | — | — |
| **Country** | | | | | | | | | | | | | | | |
| Argentina[d] | x | x | | | | x | x | | | | | | x | | |
| Bolivia[d] | x | | | | | x | | | | | | | | | |
| Brazil[a,d] | x | x | x | | x | x | x | | x | x | x | | | | |
| China[d] | | | | | | x | x | | | | | | | | |
| Colombia[d] | x | x | | | | x | x | x | x | x | x | x | x | | x |
| Costa Rica[d] | x | | x | | | x | | x | | x | | | x | | |
| Cuba[d] | x | | | | | x | | | | | | | | | |
| Dominican Republic[d] | x | | | | | x | | | | | | | | | |
| Ecuador[d] | x | | | | | x | | x | | | | | | | |
| Fiji[d] | x | | | | | x | | | | | | | | | |
| French Guiana[b] | x | | | | | x | | | | x | | | x | | |
| Gabon | x | x | | | | x | | | | | | | | | |
| Guatemala[d] | x | | | x | | x | | x | | x | | | x | x | |
| Guyana[c] | | x | | | | x | | | | | x | | x | | |
| Indonesia[d] | | | | | | x | | | | | | | | | |
| Malaysia[d] | | x | | | | | x | | | | | | | | |
| Malawi[e] | x | | | | | x | | | | x | | | | | |
| Mexico[d] | x | | | | | x | x | | x | | | | | | |
| Nigeria[d] | | | | | | x | | | | | | | | | |
| Panama[d] | x | | | | | x | x | | | | | | | | |
| Paraguay[d] | x | | | | | x | x | | | x | x | | | | |
| Peru[d] | x | | | | | x | x | | x | x | x | | | x | |
| Philippines[d] | x | | | | | x | | | | | | | | | |
| Puerto Rico[d] | x | | | | | x | | | | | | | x | | |
| Thailand[d] | x | | | | | x | | | | | | | | | |
| USA[d] | x | | | | | x | | | | | | | | | |
| Venezuela[d] | x | | | | | x | x | x | | x | x | | | | |

**GA12**

| Allele | 135 | 137 | 143 | 146 | 148 |
|---|---|---|---|---|---|
| Code | 1 | 2 | — | 3 | 4 |
| **Country** | | | | | |
| Brazil[a] | | x | x | x | x |
| French Guiana[b] | | x | x | x | x |
| Gabon | x | x | | x | x |
| Guyana[c] | | x | | x | x |

**SSR31**

| Allele | 162 | 168 | 178 | 181 | 183 | 189 | 193 | 198 |
|---|---|---|---|---|---|---|---|---|
| Code | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| **Country** | | | | | | | | |
| Gabon | x | x | x | x | x | x | x | x |

**Table C3.** (continued)

**SSR55**

| Allele | 127 | 129 | 133 | 135 | 137 | 141 | 143 |
|---|---|---|---|---|---|---|---|
| Code | 1 | 2 | 3 | 4 | — | 5 | 6 |
| **Country** | | | | | | | |
| French Guiana[b] | | x | x | x | x | x | x |
| Gabon | x | x | x | x | | x | x |

**SSR68**

| Allele | 245 | 248 | 250 | 254 | 256 | 258 | 260 | 262 | 264 | 266 | 268 | 272 | 288 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Code | 1 | — | 2 | — | 3 | — | 4 | 5 | 6 | 7 | 8 | — | 9 |
| **Country** | | | | | | | | | | | | | |
| French Guiana[b] | | x | x | x | | x | x | | x | x | x | x | x |
| Gabon | x | | x | | x | | x | x | x | x | x | | x |

**SSR169**

| Allele | 86 | 88 | 90 | 99 | 101 | 105 | 107 | 109 |
|---|---|---|---|---|---|---|---|---|
| Code | — | 1 | 2 | — | 3 | — | — | 4 |
| **Country** | | | | | | | | |
| French Guiana[b] | x | x | x | x | x | x | x | x |
| Gabon | | x | x | | x | | | x* |

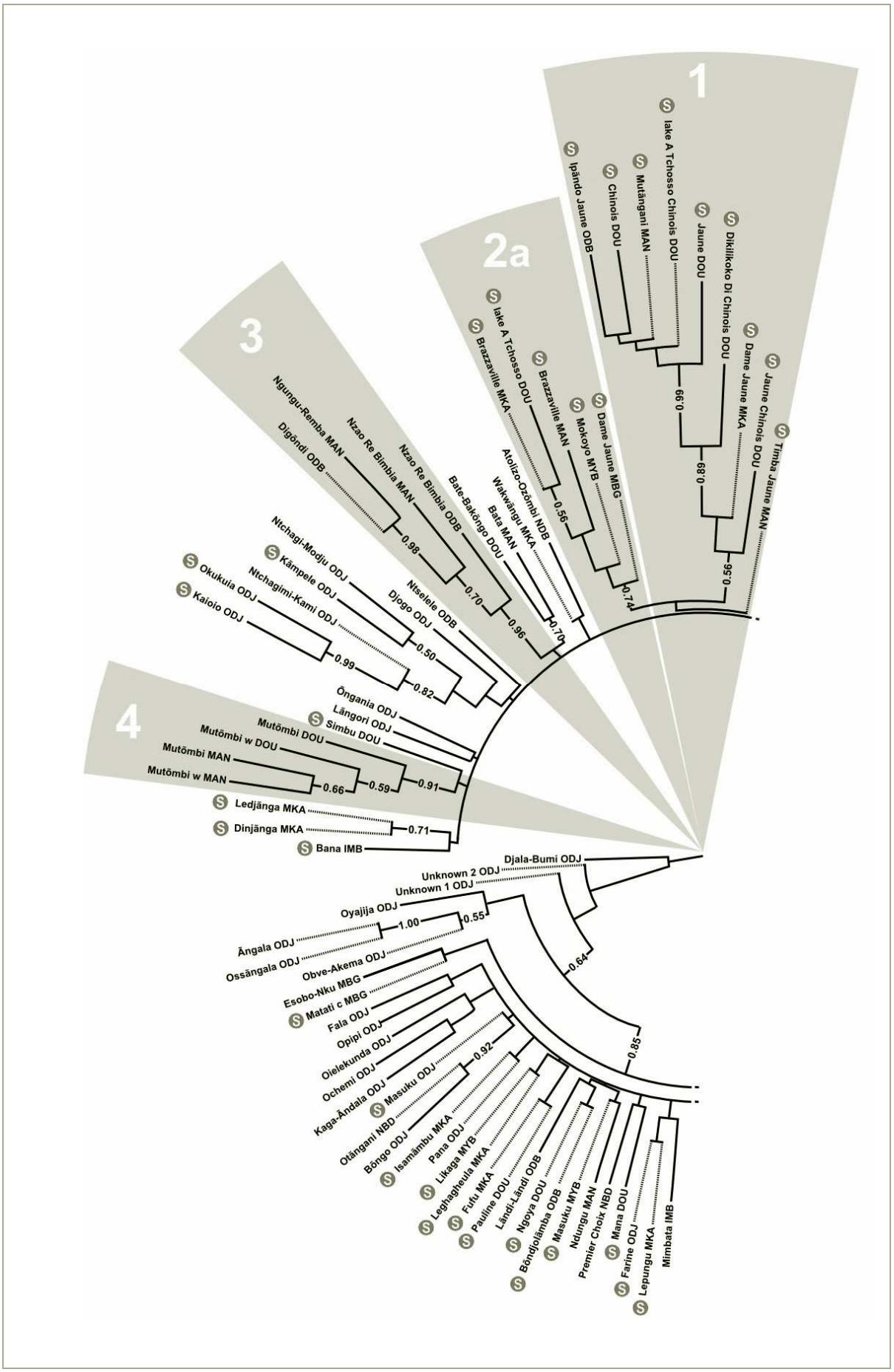
* Detected in Odjouma (see Delêtre & McKey submitted).

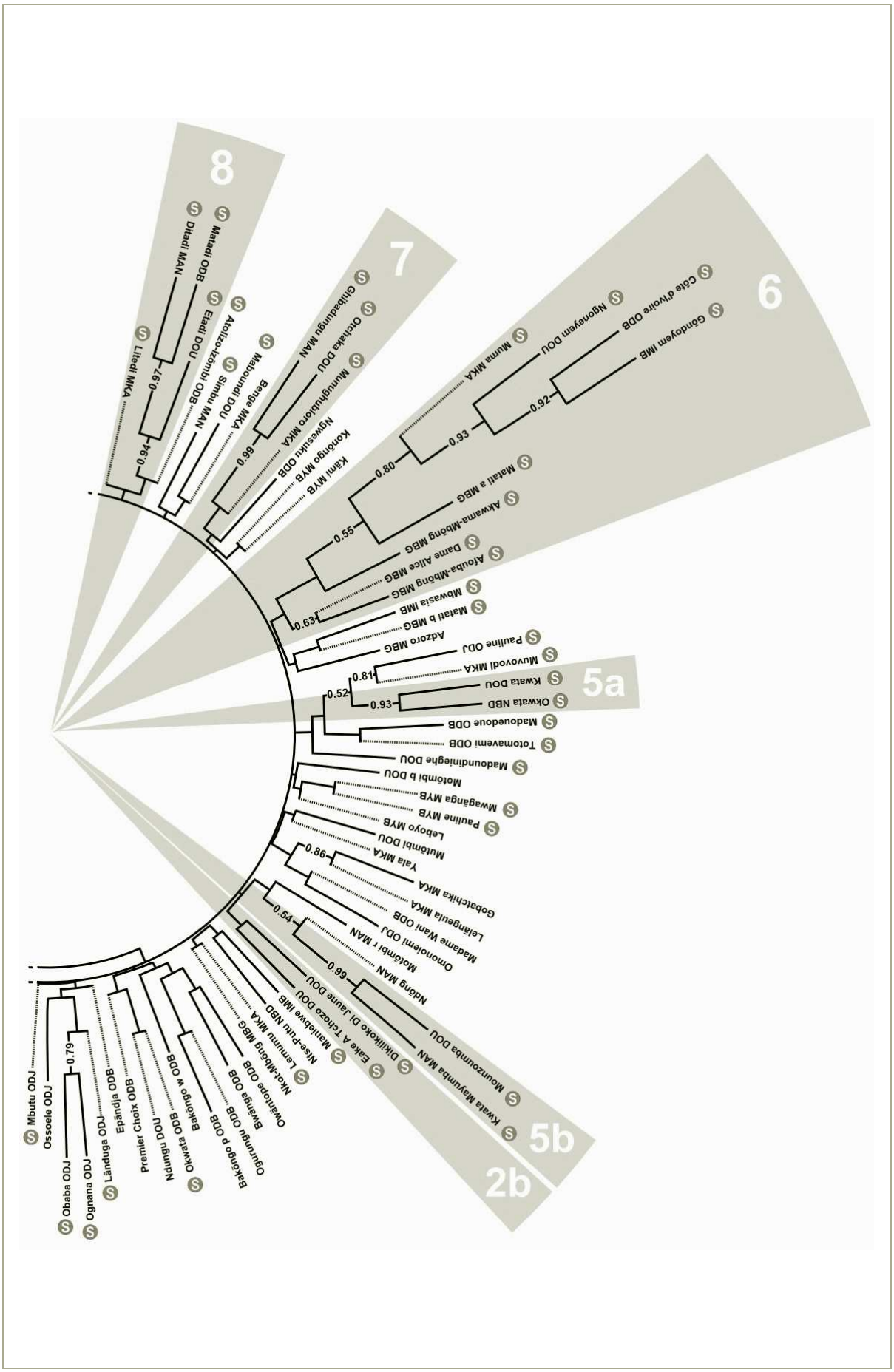
# C4. Neighbour-Joining analysis

## Methods

Patterns of diversity were characterized by analyzing the geographical patterns of distribution of manioc landraces through an analysis of synonymies and homonymies across the country. Spatial extent of clones was explored using a neighbour-joining (NJ) analysis based on Cavalli-Sforza and Edwards's (CSE) chord genetic distance (Cavalli-Sforza & Edwards 1967). Trees were computed using PHYLIP 3.69 software (Felsenstein 1989). To test the robustness of the trees, 1,000 bootstraps were performed. A consensus tree was drawn using the unweighted paired group method with arithmetic mean (UPGMA).

**Figure C2. Neighbour-Joining tree calculated from microsatellite markers** (8 loci) **and 168 landraces** ($N \geq 5$) based on Cavalli-Sforza & Edwards's chord (CSE) genetic distance (Cavalli-Sforza & Edwards 1967). Robustness of nodes was tested by performing 1,000 bootstraps. Only values >50% are shown. Eight major groups of landraces could be identified: (1) "Yellows" (landraces with yellow roots and a red stem), (2a,b) "Brazzaville" (landraces with yellow roots and a silver stem), (3) "Nzao Re Bimbia", (4) "Mutõmbi", (5a) "Kwata Mayumba" and (5b) "Kwata", (5) "Afouba-Mbõng", (7) landraces with compound leaves, and (8) "Tadi". Landraces sampled for only five plants are indicated with dotted lines. Sweet landraces are indicated with an 'S'. Villages from where the samples were collected are indicated with a three letters code: ODB (Odimba), NBD (Nombedouma), DOU (Douani), MAN (Mandilou), MAK (Makoula), MYB (Mouyabi), ODJ (Odjouma), IMB (Imbong), MBG (Mbong-Ete). The figure was split over two pages.


1
2a
3
4
Iake A Tchosso Chinois DOU
Ipāndo Jaune ODB
Chinois DOU
Mutāngani MAN
Jaune DOU
Dikilikoko Di Chinois DOU
Dame Jaune MKA
Jaune Chinois DOU
Timba Jaune MAN
Iake A Tchosso DOU
Brazzaville MKA
Brazzaville MAN
Mokoyo MYB
Dame Jaune MBG
Atolizo-Ozombi NDB
Watwāngu MKA
Bata MAN
Bate-Bakōngo DOU
Ngungu-Remba MAN
Digōndi ODB
Nzao Re Bimbia MAN
Nzao Re Bimbia ODB
Nkagi-Modju ODJ
Kāmpele ODJ
Ntchagimi-Kami ODJ
Okukuia ODJ
Kaloio ODJ
Djogo ODJ
Ntselele ODB
Ōngania ODJ
Lāngori ODJ
Simbu DOU
Mutōmbi DOU
Mutōmbi w DOU
Mutōmbi MAN
Mutōmbi w MAN
Ledjānga MKA
Dinjānga MKA
Bana IMB
Djala-Bumi ODJ
Unknown 2 ODJ
Unknown 1 ODJ
Oyajija ODJ
Āngala ODJ
Ossāngala ODJ
Obve-Akema ODJ
Esobo-Nku MBG
Matati c MBG
Fala ODJ
Opipi ODJ
Oielekunda ODJ
Ochemi ODJ
Kaga-Āndala ODJ
Masuku ODJ
Otāngani NBD
Bōngo ODJ
Isamāmbu MKA
Pana ODJ
Likaga MYB
Leghagheula MKA
Fufu MKA
Pauline DOU
Lāndi-Lāndi ODB
Ngoya DOU
Bōndjolamba ODB
Masuku MYB
Ndungu MAN
Premier Choix NBD
Mana DOU
Farine ODJ
Lepungu MKA
Mimbata IMB
0.66
0.89
0.56
0.74
0.56
0.70
0.96
0.70
0.98
0.70
0.50
0.99
0.82
0.66
0.59
0.91
0.71
1.00
0.55
0.64
0.85
0.92


8
7
6
5a
5b
2b
Matadi ODB
Ditadi MAN
Etadi DOU
Litedi MKA
Atizizotshitshi ODB
Simbu MAN
Mabounti DOU
Benga MKA
Gnibadungu MAN
Otchaka DOU
Mfungubiboro MKA
Ngwasuku ODB
Kontongo MYB
Kami MYB
Côte d'Ivoire ODB
Ngonoyem DOU
Gondoyem IMB
Mima MKA
Matati a MBG
Akwama-Mbong MBG
Dame Alice MBG
Afouba-Mbong MBG
Mbwasia IMB
Matati b MBG
Adzoro MBG
Pauline ODJ
Muvovoi MKA
Kwata DOU
Okwata NBD
Madoudoue ODB
Totomayemi ODB
Madoundinegbe DOU
Motombi b DOU
Mwagbanga MYB
Pauline MYB
Leboyo MYB
Mutombi DOU
Yala MKA
Gobatchika MKA
Lelangeula MKA
Madame Wani ODB
Omonolemi ODJ
Motombi r MAN
Ndong MAN
Mouzoumba DOU
Kwata Mayumba MAN
Dikilikoko Di Jaune DOU
Eake A Tchozo DOU
Matebowe IMB
Nkot-Mbong MBG
Lemmum MKA
Nise-Puu NBD
Bwanga ODB
Ovambope ODB
Ogumungu ODB
Bakongo p ODB
Bakongo w ODB
Okwata ODB
Nkungu DOU
Premier Choix ODB
Epandja ODB
Landuga ODJ
Ognana ODJ
Obaba ODJ
Ossoele ODJ
Mbutu ODJ
0.97
0.94
0.99
0.55
0.80
0.63
0.93
0.92
0.81
0.52
0.93
0.86
0.54
0.99
0.79

# C5. Bayesian clustering analysis

## Methods

Genetic data are available for ten villages (Table C4.1). The Bayesian clustering method implemented in the R-package GENELAND version 3.1.4 (Guillot *et al.* 2005a) was used to detect geographical discontinuities in manioc genetic diversity at the scale of the entire country. GENELAND does not assume admixture (*i.e.*, individuals are discretely distributed among inferred populations) and uses the genetic and geographic information of each sampling unit, with no prior assumptions about population groups or boundaries, to infer *K*, the number of clusters in the data. Because the method implemented in GENELAND assumes a spatial mixture of panmictic populations, clonal replicates were removed from the data set (treating each study site independently), leading to a total of 398 distinct multilocus genotypes (Table C4.2). All analyses were performed considering the eight loci common to the maximum number of study sites. Only for comparison, the same analysis was run with 6 loci (all ten study sites) and 10 loci (excluding Mopia and Odjouma).

**Table C4.1. Study sites, number of farmers interviewed (*N*), number of farms surveyed (*F*), number of landraces sampled (*V*), number of samples (*S*) collected and number of loci characterized (*L*)**.

| Village | Longitude | Latitude | *N* | *F* | *V* | *S* | *L* |
|---|---|---|---|---|---|---|---|
| Odimba | 00°47’28.3”S | 009°09’50.0”E | 12 | 22 | 21 | 282 | 10 |
| Nombedouma | 00°55’08.3”S | 010°02’43.4”E | 14 | 27 | 5 | 70 | 10 |
| Douani | 01°02’41.4”S | 010°40’59.5”E | 15 | 21 | 24 | 438 | 10 |
| Mandilou | 01°17’17.2”S | 010°36’47.3”E | 18 | 25 | 15 | 120 | 10 |
| Makoula | 01°20’24.8”S | 012°25’27.3”E | 16 | 23 | 18 | 100 | 10 |
| Mopia | 01°49’09.1”S | 013°36’10.3”E | 21 | 31 | 10 | 62 | 8[a] |
| Mouyabi | 02°14’23.5”S | 013°34’31.6”E | 15 | 17 | 8 | 35 | 10 |
| Odjouma | 01°06’06.4”S | 014°24’37.9”E | 31 | 127 | 30 | 465 | 8[b] |
| Imbong | 01°02’19.3”N | 013°59’54.5”E | 21 | 29 | 10 | 53 | 10 |
| Mbong-Ete | 02°08’17.9”N | 011°29’56.7”E | 28 | 66 | 8 | 270 | 10 |
| **Total** | | | 191 | 388 | 149 | 1895 | |

a. Samples not characterized for SSR31 and SSR169.
b. Samples not characterized for GAGG5 and GA134.

**Table C4.2. Geographical coordinates and number of distinct genotypes (*N*)** for each study site included in the country-wide analysis of manioc genetic diversity in Gabon. Mopia (site 6), for which the loci SSR31 and SSR169 were not typed, was excluded from the analyses.

| Village | Ethnic group | Longitude | Latitude | *N* |
|---|---|---|---|---|
| Odimba | Orungu [B.11b] | 00°47’28.3”S | 009°09’50.0”E | 43 |
| Nombedouma | Galwa [B.11c] | 00°55’08.3”S | 010°02’43.4”E | 48 |
| Douani | Tsogho [B.31] | 01°02’41.4”S | 010°40’59.5”E | 57 |
| Mandilou | Ghisir [B.41] | 01°17’17.2”S | 010°36’47.3”E | 45 |
| Makoula | Ndzabi [B.52] | 01°20’24.8”S | 012°25’27.3”E | 43 |
| Mopia | Kaninigi [B.602] | 01°49’09.1”S | 013°36’10.3”E | — |
| Mouyabi | Bongo [Pygmy] | 02°14’23.5”S | 013°34’31.6”E | 16 |
| Odjouma | Teke [B.71] | 01°06’06.4”S | 014°24’37.9”E | 80 |
| Imbong | Kwele [A.85b] | 01°02’19.3”N | 013°59’54.5”E | 18 |
| Mbong-Ete | Ntumu [A.75a] | 02°08’17.9”N | 011°29’56.7”E | 48 |
| **Total** | | | | 398 |

Five independent runs were performed with 100,000 Markov-Chain Monte Carlo (MCMC) iterations, of which every hundredth one was saved. *K*, the number of genetic clusters tested, was set to vary between a minimum value fixed to 1 and a maximum value fixed to 9, the number of study sites included in the analyses. The Dirichlet spatial model for allelic frequencies (D-model), which assumes uncorrelated allelic frequencies across sites and proved to perform better than the alternative F-model (correlated frequencies) in detecting subtle genetic structures (Guillot *et al.* 2005b), was used as a prior for allele frequencies. The maximum rate of Poisson process was fixed to 100 and the maximum number of nuclei in the Poisson–Voronoi tessellation was fixed to 300. No uncertainty was attached to spatial coordinates. Posterior probabilities of population membership for each pixel of the spatial domain were computed using a burn-in period length of 500 iterations. Pairwise genetic differentiation ($F_{ST}$) was calculated between the clusters identified by GENELAND, using FSTAT 2.9.3 (Goudet 1995).

Each cluster was characterized using standard population genetic statistics. Allelic frequencies, *F*-statistics (Weir & Cockerham 1984), observed ($H_O$) and expected ($H_E$) heterozygosity (Nei 1978) were computed using FSTAT 2.9.3 (Goudet 1995). For comparison between villages, allelic richness ($\hat{A}$) was estimated after clonal replicates were removed from the samples (treating each village independently) and the sample size standardized to a common threshold of 15, 30 and 45 MLGs, using the multiple random reduction method proposed by Leberg (2002). Polymorphism information content (*PIC*) was calculated for each marker using the Botstein *et al.* (1980) formula:

$$PIC = 1 - \sum_{i=1}^{n} pi^2 - 2\left[\sum_{i=1}^{n-1}\sum_{j=i+1}^{n} pi^2\, pj^2\right] \qquad [1]$$

where $p_i$ is the frequency of the *i*th allele, and *n* the total number of alleles.

## Results

*Structure of manioc genetic diversity in Gabon.* Assuming uncorrelated allelic frequencies (D-model), GENELAND inferred three distinct genetic clusters* (Figure C4.1a): (1) a south-western cluster, which encompassed all sites from 1 to 7; (2) an eastern cluster (site 8); and (3) a northern cluster, which encompassed sites 9 and 10. All three clusters showed low but significant genetic differentiation (Table C4.3). Allelic richness ($\hat{A}$) was significantly lower in the northern cluster (one-way ANOVA followed by Tukey's *post-hoc* test, $F = 189.7$, df = 2, $P < 10^{-4}$).

**Table C4.3. $H_O$ (observed heterozygosity) and $H_E$ (expected heterozygosity), $\hat{A}$ (allelic richness, estimated after standardization of $N$ to a common threshold of 50 MLGs), $A_p$ (number of private alleles), $F_{IS}$ (fixation index), and pairwise $F_{ST}$ for the northern, eastern and south-western clusters identified by GENELAND.**

| | | | | | | | *Pairwise* $F_{ST}$ | |
|---|---|---|---|---|---|---|---|---|
| **Cluster** | $H_O$ | $H_E$ | $N$ | $\hat{A}$ | $A_p$ | $F_{IS}$ | *Eastern* | *Northern* |
| *South-Western* | 0.666 | 0.628 | 252 | 4.9 ± 0.2 | 4 | -0.058** | 0.038** | 0.052** |
| *Eastern* | 0.733 | 0.637 | 66 | 4.8 ± 0.2 | 5 | -0.144** | | 0.055** |
| *Northern* | 0.689 | 0.604 | 80 | 4.3 ± 0.1 | 0 | -0.130** | | |

** $P$-value < 0.01.

When the alternative F-model was used (assuming correlated frequencies), finer subdivisions could be identified within the south-western cluster, which could be divided into three clusters (Table C4.4): "Ogooué" (encompassing sites 1 and 2), "Du Chaillu" (sites 3, 4 and 5), and "South Congo" (site 7), while the northern cluster ("Cameroon") and the eastern cluster ("East Congo") did not change (Figure C4.1b).

**Table C4.4. $H_O$ (observed heterozygosity) and $H_E$ (expected heterozygosity), $\hat{A}$ (allelic richness, estimated after standardization of $N$ to a common threshold of 50 MLGs), $A_p$ (number of private alleles), $F_{IS}$ (fixation index), and pairwise $F_{ST}$ for the five clusters identified by GENELAND under the F-model.**

| | | | | | | | *Pairwise* $F_{ST}$ | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Cluster** | $H_O$ | $H_E$ | $N$ | $\hat{A}$ | $A_p$ | $F_{IS}$ | *Du Chaillu* | *South Congo* | *East Congo* | *Cameroon* |
| *Ogooué* | 0.681 | 0.646 | 91 | 4.3 ± 0.2 | 1 | -0.050** | 0.014** | 0.011** | 0.033** | 0.049** |
| *Du Chaillu* | 0.653 | 0.601 | 145 | 4.3 ± 0.2 | 1 | -0.083** | | 0.022** | 0.049** | 0.061** |
| *South-Congo* | 0.695 | 0.656 | 16 | 4.8 ± 0.1 | 1 | -0.028* | | | 0.024** | 0.054** |
| *East Congo* | 0.733 | 0.637 | 80 | 4.1 ± 0.2 | 5 | -0.144** | | | | 0.055** |
| *Cameroon* | 0.689 | 0.605 | 66 | 3.8 ± 0.2 | 1 | -0.130** | | | | |

* $P$-value < 0.05; ** $P$-value < 0.01.

* Consistent results were obtained using the ten loci (data not shown).

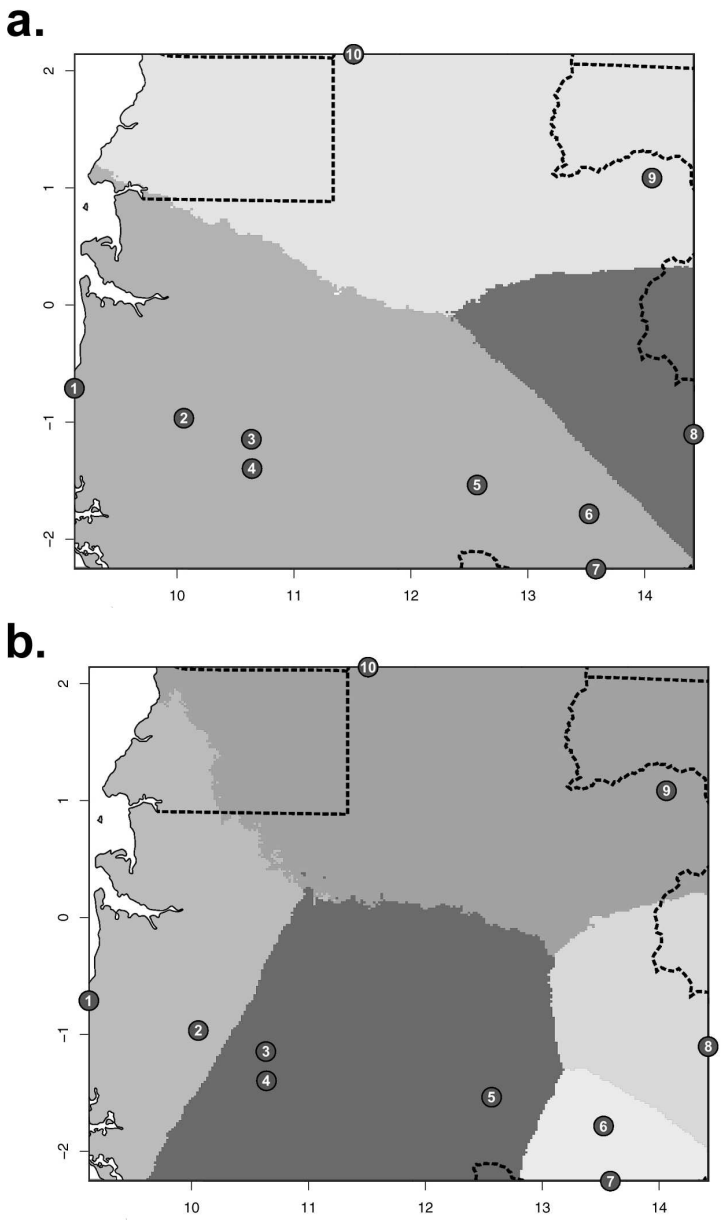



**Figure C4.1. Posterior mode of population membership** (a) **for the "south-western", "northern", and "eastern" clusters** inferred by GENELAND under the D-model (assuming uncorrelated allelic frequencies between sites); (b) **posterior mode of population membership for the five clusters** inferred by GENELAND under the F-model (correlated allelic frequencies). Study sites (❶ to ❿) are reported on the maps. The unit of coordinates on the x and y axes is decimal degree.

*Allelic characterization of the clusters.* Figure C4.2 below illustrates the geographical patterns of distribution of manioc allelic diversity in Gabon. There was no particular pattern associated with the markers GAGG5 and GA134, both of which showed overall little polymorphism (*PIC* = 0.374 and *PIC* = 0.256, respectively). However, one allele, $GA134_{325}$, was only found in villages where yellow varieties were grown (Table C4.5).

**Table C4.5. Frequency of the allele $GA134_{325}$ in the ten villages surveyed.**

| Cluster | | Village | Landraces | Frequency |
|---|---|---|---|---|
| ***South-Western*** | *Ogooué* | Odimba | — | (absent) |
| | | Nombedouma | — | (absent) |
| | *Du Chaillu* | Douani | '*Jaune Chinois*'<br>'*Iake A Tchosso*'<br>'*Dikilikoko Di Jaune*'<br>'*Eakea A Tchozo*'<br>'*Maboundi*' | 3.2% |
| | | Mandilou | '*Brazzaville*' | 2.9% |
| | | Makoula | '*Benge*' | 2.0% |
| | *South Congo* | Mopia | '*Wokwãngu*' | (not sampled) |
| | | Mouyabi | '*Mokoyo*' | 1.6% |
| ***Eastern*** | *East Congo* | Odjouma | — | (absent) |
| ***Northern*** | *Cameroon* | Imbong | '*Dame Jaune*' | (not sampled) |
| | | Mbong-Ete | '*Madame Jaune*' | <1% |

GA12 (*PIC* = 0.526) showed similarly little variation among regions, with the allele $GA12_{137}$ accounting for 54.1% of the locus polymorphism. One allele ($GA12_{139}$, <1%) was however found only in Odjouma (eastern cluster), and one allele, ($GA12_{135}$, <1%) was private to Mandilou (south-western cluster)

GA21 (*PIC* = 0.441) showed in contrast a clear-cut differentiation between the south-western cluster and the eastern and northern clusters inferred by GENELAND. The allele $GA21_{118}$ was present in all villages below the Ogooué (forming a virtual NW-SE boundary between the **ghõngo** and **õndo** linguistic domains), but in none of the villages located above this line (Table C4.6). Similarly, $GA21_{110}$ and $GA21_{112}$ have contrasted frequency distributions both sides of the Ogooué.

**Figure C4.2. Distribution of allelic frequencies in Gabon**. The presence of an allele is indicated by a dot, whose diameter represents the frequency of the allele. Mopia, which was not typed for SSR31 and SSR169, was included for comparison only.

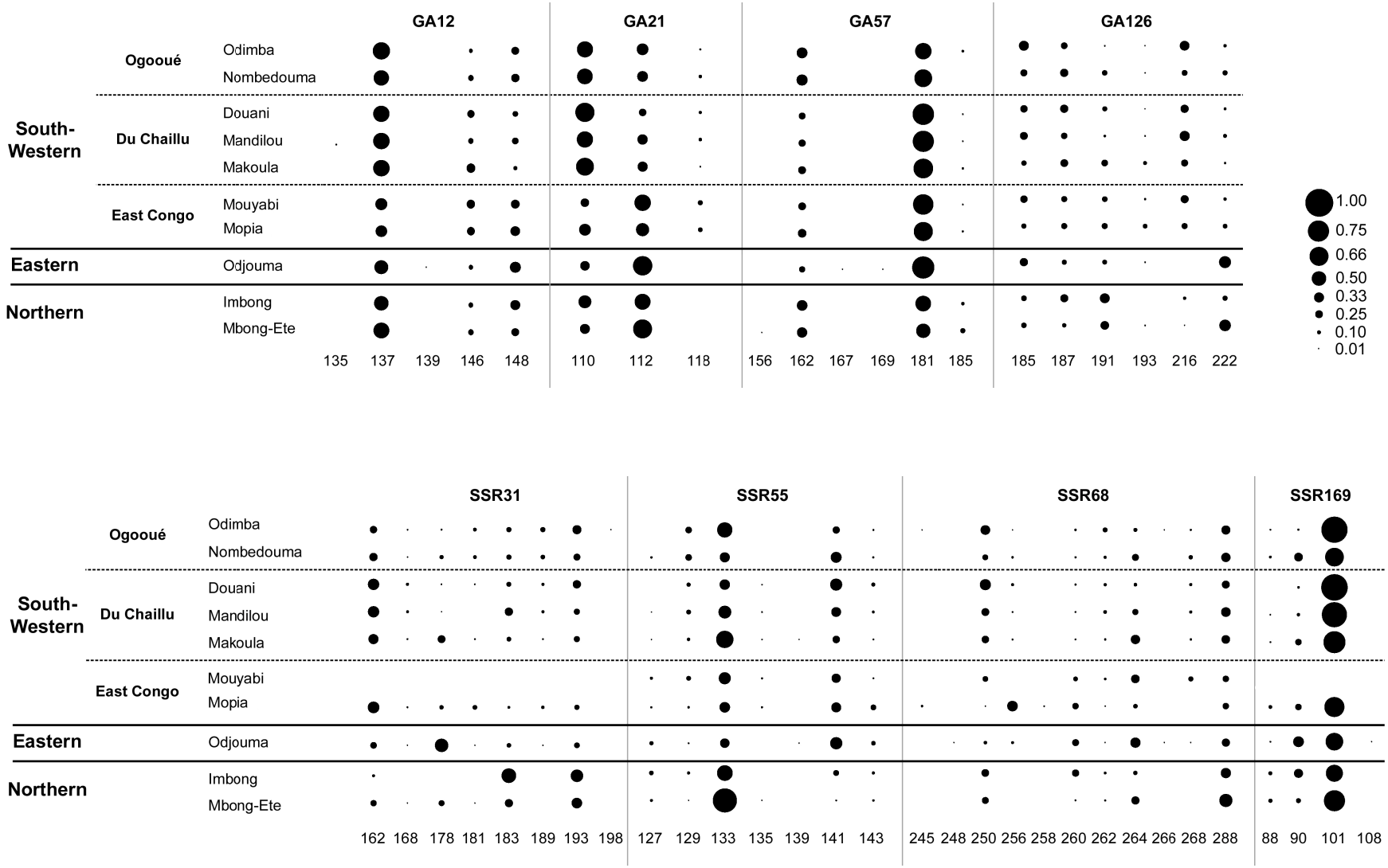

GA12
GA21
GA57
GA126
South-Western
Ogooué
Odimba
Nombedouma
Du Chaillu
Douani
Mandilou
Makoula
East Congo
Mouyabi
Mopia
Eastern
Odjouma
Northern
Imbong
Mbong-Ete
135 137 139 146 148
110 112 118
156 162 167 169 181 185
185 187 191 193 216 222
1.00
0.75
0.66
0.50
0.33
0.25
0.10
0.01
SSR31
SSR55
SSR68
SSR169
162 168 178 181 183 189 193 198
127 129 133 135 139 141 143
245 248 250 256 258 260 262 264 266 268 288
88 90 101 108

**Table C4.6. Frequency of the allele $GA21_{118}$ in the ten villages surveyed.**

| Cluster | | Village | Landraces | Frequency |
|---|---|---|---|---|
| ***South-Western*** | *Ogooué* | Odimba | '*Bakõngo*'<br>syn. '*Ogurungu*' | 3.9% |
| | | Nombedouma | '*Atolizo Ozõmbi*'<br>'*Evizovizo*'<br>'*Laurence*'<br>'*Loulou*'<br>'*Mpiza-Vizue*'<br>'*Nzoghou*'<br>'*Okwata*'<br>'*Otãngani*'<br>'*Premier Choix*'<br>'*Yamoughe*' | 9.3% |
| | *Du Chaillu* | Douani | '*Kwata*'<br>'*Mounzoumba*'<br>'*Ndungu*' | 8.6% |
| | | Mandilou | '*Kwata Mayumba*'<br>'*Bata*' | 9.1% |
| | | Makoula | '*Wakwãngu*' | 3.0% |
| | *South Congo* | Mopia | '*Wokwãngu*' | 15.0% |
| | | Mouyabi | '*Kãmi*'<br>'*Konõngo*' | 14.1% |
| ***Eastern*** | *East Congo* | Odjouma | — | (absent) |
| ***Northern*** | *Cameroon* | Imbong | — | (absent) |
| | | Mbong-Ete | — | (absent) |

The locus GA57 (*PIC* = 0.413) showed similarly marked differences between geographical areas. The allele $GA57_{185}$ was more prevalent in the northern cluster (15%), where it was associated with the landrace '*Afouba-Mbõng*' (Mbong-Ete), synonymous of the landraces '*Gõndoyem*' (Imbong), '*Muma*' (Makoula) and '*Côte d'Ivoire*' (Odimba). $GA57_{185}$ was completely absent from the eastern cluster. Conversely, $GA57_{167}$ and $GA57_{169}$, both rare (frequency < 1%), were private to the eastern cluster (Odjouma).

Although highly polymorphic, no particular pattern was found for GA126 (*PIC* = 0.776). The allele $GA126_{193}$, which was not sampled in Imbong, was however systematically associated with bitter landraces (Table C4.7), except in Mbong-Ete where it was also found, however in low frequency, in sweet manioc ('*Afouba-Mbõng*').

SSR31 showed the highest polymorphism in Gabon (*PIC* = 0.767). $SSR31_{162}$ was more frequent in the south-western cluster, while $SSR31_{183}$ and $SSR31_{193}$ were more frequent in the northern cluster. In the eastern cluster (Odjouma), $SSR31_{178}$ accounted for 47% of the locus polymorphism. Three alleles, $SSR31_{168}$, $SSR31_{178}$, and $SSR31_{181}$, were missing in Imbong and in low frequencies in Mbong-Ete.

**Table C4.7. Frequency of the allele $GA126_{193}$ in the ten villages surveyed.**

| Cluster | | Village | Landraces | Frequency |
|---|---|---|---|---|
| ***South-Western*** | *Ogooué* | Odimba | '*Madame Wani*' | <1% |
| | | Nombedouma | '*Loulou*'<br>'*Ngu'u*' | 1.4% |
| | *Du Chaillu* | Douani | '*Motõmbi*' | 1.0% |
| | | Mandilou | '*Ndungu*'<br>'*Simbu*' | 2.9% |
| | | Makoula | '*Gobatchika*' | 11.0% |
| | *South Congo* | Mopia | '*Mwagãnga*' | 5.0% |
| | | Mouyabi | '*Kãmi*' | 14.1% |
| ***Eastern*** | *East Congo* | Odjouma | '*Opipi*'<br>'*Omonoiemi*' | 2.7% |
| ***Northern*** | *Cameroon* | Imbong | — | (absent) |
| | | Mbong-Ete | '*Adzoro*'<br>'*Afouba-Mbõng*' | 2.9% |

In Mbong-Ete, SSR55 (*PIC* = 0.595) had the lowest polymorphism level (*PIC* = 0.261), with the allele $SSR55_{133}$ accounting for 84.7% of the locus polymorphism. The alleles $SSR55_{141}$ and $SSR55_{143}$, both very common in the rest of Gabon (43% and 11% respectively in the eastern cluster, and 33% and 8%, respectively, in the south-western cluster), were present only in low frequency (5%) in Mbong-Ete. In addition, the frequency of the allele $SSR55_{129}$ decreased with the distance from the Ogooué.

Several alleles of the locus SSR68 (*PIC* = 0.749) were also missing in the northern cluster. $SSR68_{268}$, present in all villages of the south-western cluster (7%), was missing in Imbong and Mbong-Ete, and rare in the eastern cluster (1%). Similarly, $SSR68_{256}$, which was found in particularly high frequency in Mouyabi (36%), was missing in Imbong and Mbong-Ete. The eastern cluster inferred by GENELAND was also characterized by the unique presence of the allele $SSR68_{248}$.

SSR169 (*PIC* = 0.251), finally, showed low polymorphism and no particular pattern of diversity across the country. $SSR169_{101}$ accounted for 84.5% of the locus polymorphism. One allele, $SSR169_{108}$, rare (<1%) and private to the landrace '*Õndzalapaki*', was detected only in the eastern cluster (Odjouma).

# Glossary

# D1. Glossary

**D1. Definition of terms**. For terms borrowed to anthropology, I relied on the definition given by Bonte and Izard (1991) in their *Dictionnaire de l'ethnologie et de l'anthropologie*.

**Bottle-neck**. From a genetic point of view, introductions often result in a loss of diversity, as only a sub-sample of the total genetic diversity present in the area of origin is transferred to the new area. The reduction in population size is called 'bottleneck'.

**Clan**. A group of people belonging to the same filiation or lineage (*i.e.*, sharing a common ancestor). In Gabon, with the noticeable exception of the Fang (see Chapter V), all groups are matrilineal; membership of the clan is inherited from the mother.

**Cultivar**. A variety that has been created and/or selected through formal breeding.

**Ethnic group**. There is no clear definition attached to the notion of ethnicity, and I chose to favour Barth's (1969) view that it is the maintenance of social boundaries, which define ascription of a member to the group and exclusion of others, that ensures the continuity of the ethnic identity. Because of the dynamic nature of cultural accretion, the continuation of these boundaries in time implies the preservation of a limited set of cultural factors that define the cultural difference between members and non-members of the group. As the culture evolves, the definitional traits of the culture may also change, as long as they maintain a difference that defines these boundaries (e.g., the Myènè [B.11]; see Chapter III). In other words, ethnicity is the definition of a "category of ascription and identification" by the people themselves. In this thesis, I chose to consider the language as this boundary, and referred to ethnic groups by their language, using the revision of Guthrie's classification of Bantu languages (Guthrie 1948) as proposed by Maho (2003).

**Farm**. Farm is understood here as the set of fields (parcels or plots) managed by a single farmer.

**Farming system**. The sets of rules and techniques related to the preparation and management of a set of fields. The farming system is characterized in space and time by the sequence of farming activities (clearing, burning, planting, weeding, and harvest) and by the crops associated with it.

**Founder effect**. The loss of variation that follows when an original population splinters into smaller populations, each of which contains only a sub-sample of the diversity present in the original population. Allelic frequencies in the new populations are generally unrepresentative of allelic frequencies in the population of origin.

**Genetic drift**. The changes in relative allelic frequencies due to stochastic events (random sampling).

**Homoplasy**. Two alleles can be similar as a result of convergent evolution, but have independent origins. Because of the high mutation rate of microsatellites, relatively high level of homoplasy may exist. Homoplasy leads to the underestimation of total variation and genetic distance, and to an overestimation of the similarities among populations.

**Landrace**. In this thesis, I adopted Harlan's (1975) definition of landraces: "Landraces have a certain genetic integrity. They are recognizable morphologically; farmers have names for them and different landraces are understood to differ in adaptation to soil type, time of seeding, date of maturity, height, nutritive value, use and other properties. Most important, they are genetically diverse".

**Large allele dropout**. Preferential amplification of shorter alleles (also known as short allele dominance). Large allele dropout are suggested when the allele-size range exceeds 150bp, and can result in an apparent deficiency in heterozygotes.

**MLG**. Acronym of MultiLocus Genotype.

**Named diversity**. The number of categories of manioc identified and named by farmers. Named diversity is a highly biased evaluation of diversity at any level considered, as it is highly subjective and doesn't necessarily match genetic diversity.

**Null allele**. For microsatellite markers, non-amplification during the PCR of an allele caused by a mutation in the flanking regions that prevents one or both primers from binding. Null alleles are non-amplified alleles that, when segregating with another allele, result in an apparent homozygote. The presence of null alleles thus leads to an overestimation of observed homozygosity.

**Singleton**. A unique genotype, not shared by any other individual plant.

**Stutter band**. During PCR amplification of DNA, amplification creates DNA fragments that are one or several repeats shorter than the actual allele. Stutter bands are quite common for dinucleotide repeats. The presence of stutter bands is suggested when there is a deficiency of heterozygotes with one repeat difference between both alleles.

**Tribe**. In this thesis, tribe is used as a synonym of ethnic group.

**Varietal diversity**. The local diversity of landraces emically identified.